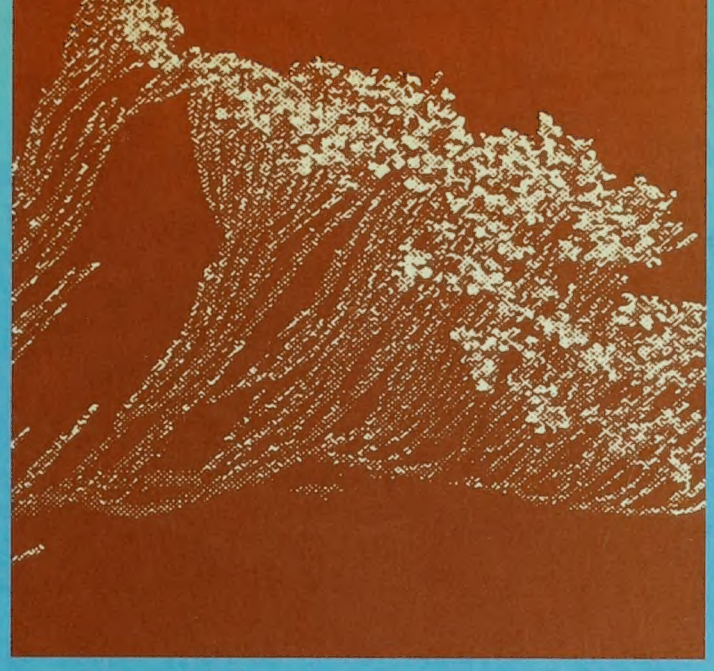
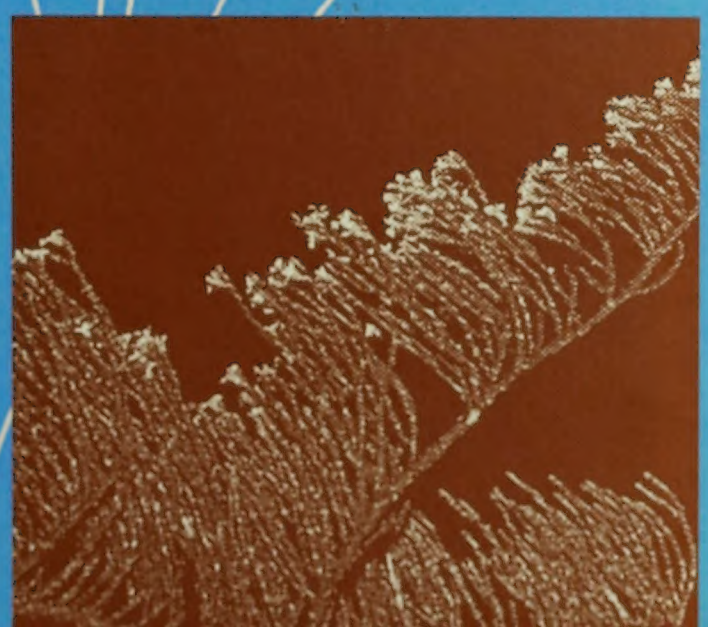


. Claßen-Bockhoff

INFLORESCENCES IN BRUNIACEAE



Opera Botanica Belgica 12

Selected abbreviations

az	**a**pical **z**one
bz	**b**ranching **z**one
cfL	**c**ataleptic **f**lowering **L**ateral shoot
cfR	**c**ataleptic **f**lowering **R**enewal shoot
cR	**c**ataleptic **R**enewal shoot
dL	**d**eterminate **L**ateral shoot
En	***En**richment*
fz	**f**lowering **z**one
H	***H**omogenization*
ipi	**i**nflorescence **p**rimordium **i**nhibited
iL	**i**ndeterminate **L**ateral shoot
L	**L**ateral shoot
li	**l**ateral **i**nflorescence
lia	**l**ateral **a**ggregate of inflorescences
mc	**m**onopodial **c**onnection
me	**me**sotony/mesotonic
n	growth period, season
R	**R**enewal shoot
RS	**R**eference **S**ystem
RU	**R**eproductive **U**nit
rz	**r**enewal **z**one
rz-1	**r**enewal **z**one of the parent axis
sc	**s**ympodial **c**onnection
sfL	**s**ylleptic **f**lowering **L**ateral shoot
sfR	**s**ylleptic **f**lowering **R**enewal shoot
SGU	**S**easonal **G**rowth **U**nit
SU	**S**ympodial **U**nit
svL	**s**ylleptic **v**egetative **L**ateral shoot
svR	**s**ylleptic **v**egetative **R**enewal shoot
T	***T**runcation*
tf	**t**erminal **f**lower
ti	**t**erminal **i**nflorescence
tia	**t**erminal **a**ggregate of inflorescences
vz	**v**egetative **z**one
I, II, ..	orders of branches
', '', ..	orders of lateral structures/processes

Symbols

flower

inflorescence

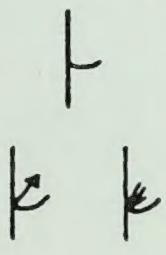
aggregate of inflorescences

flower/inflorescence in bud

flower/inflorescence deflorated

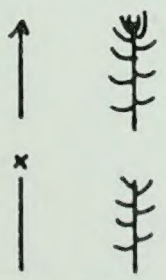
flowers/fruits fallen off

organs fallen off, missing



node with leaf

node with leaf and axillary bud



shoot with active apical meristem

shoot with inhibited apex

shoot broken off, damaged

shoot in graph interrupted

shoot in graph extended in length

Selected abbreviations and symbols,
see inside cover.

21 AUG. 2000

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Volume 12

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WITH GENERAL COMMENTS ON INFLORESCENCES IN WOODY PLANTS

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Opera Botanica Belgica **12**

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R. Claßen-Bockhoff

Inflorescences in Bruniaceae

With general comments on inflorescences in woody plants

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Contents

p.		
7		Preface and Acknowledgements
9		Summary
11	**1**	**Introduction**
11	1.1	Bruniaceae, a southern family
14	1.2	The infrageneric relationships and the systematic position of the Bruniaceae
17	**2**	**Material and methods**
17	2.1	Material
21	2.2	Methods
21	2.2.1	Procedure
21	2.2.2	Glossary
23	2.2.3	Abbreviations
24	2.2.4	Symbols
25	**3**	**Structure and position of the inflorescences**
25	3. 1	*Audouinia*
33	3. 2	*Berzelia*
71	3. 3.	*Brunia*
101	3. 4	*Linconia*
107	3. 5	*Lonchostoma*
117	3. 6	*Mniothamnea*
127	3. 7	*Nebelia*
149	3. 8	*Pseudobaeckea*
163	3. 9	*Raspalia*
189	3.10	*Staavia*
209	3.11	*Thamnea*
221	3.12	*Tittmannia*
233	**4**	**Inflorescences in woody plants**
233	**4.1**	**Basic questions in comparing inflorescences in woody plants**
233	4.1.1	The example of the Bruniaceae
235	4.1.2	The problem of finding an appropriate reference system
235	4.1.3	The problem of finding the reproductive unit

239	**4.2**	**A short history of morphological concepts and disputes**
239	4.2.1	Inflorescences and woody plants: early concepts
239	4.2.2.1	The concept of Parkin
241	4.2.1.2	The concept of Pilger
243	4.2.2.	Wilhelm Troll and his time
243	4.2.2.1	The typological concept of synflorescences
246	4.2.2.2	The dynamic concept of cyclic evolution
248	4.2.3	Current views on inflorescence morphology
248	4.2.3.1	Typology, terminology and the question of homology
250	4.2.3.2	Inflorescences, synflorescences and flowering shoot systems in woody plants
257	4.2.3.3	`Uniflorescences´ and `conflorescences´ sensu Briggs & Johnson
259	4.2.3.4	`L´unité de floraison´ sensu Sell
261	4.2.4	Architectural studies in woody plants
262	4.2.4.1	Longitudinal symmetry and the position of inflorescences
265	4.2.4.2	Architectural models, constructional units and the concept of neoteny
272	4.2.5	Summary
275	**4.3**	**The `brunioid´ reference framework**
275	4.3.1	The architecture of Bruniaceae
277	4.3.2	The `brunioid´reference system
278	4.3.2.1	Plasticity of the reference system in Bruniaceae
280	4.3.2.2	The reference system tested against other plant groups
281	4.3.3	Reproductive units
281	4.3.3.1	Definition and delimitation
283	4.3.3.2	The reproductive units in Bruniaceae
285	4.3.3.3	Reproductive units in other plant groups
286	4.3.4	The analogous nature of `proliferation
287	4.3.5	A short comment on the evolution of inflorescences
291	**5**	**Systematic conclusions from inflorescence morphology**
291	5.1	Position and organization of the individual RUs in Bruniaceae
291	5.1.1	Position of the RU
295	5.1.2	Organization of the RU
297	5.2	The intergeneric relationships of the Bruniaceae
303	5.3	Outlook
305	**6**	**References**

Preface and Acknowledgements

When I visited the Cape Province for the first time in 1987 I was surprised by the high diversity of the Bruniaceae. The flowerlike inflorescences of the genera *Staavia* and *Nebelia* had aroused my interest, but after having seen several species in their natural habitats, I decided to study the inflorescence morphology of the family in more detail. I did not know what lay in store for me!

As many of the species are rare and occur in inaccessible locations on the top of the mountains it was not only physically difficult to reach their habitats, and frustrating to find out that the expected population no longer existed but absolutely impossible to locate the plants without the generous help of the South African colleagues and forest managers.

For that reason my first thanks are addressed to all who have stood by me in word and deed: to Prof. Dr. Anthony Hall (Bolus Herbarium, University of Cape Town), with whom I have corresponded over many years and who critically reviewed my first manuscript, to Dr. John Rourke (Compton Herbarium, Kirstenbosch), who provided me with working facilities at the Herbarium and arranged several field trips for me, and to all the other colleagues from the Compton Herbarium who have kindly supported my studies, e.g. Dr. Dee Paterson-Jones, Dr. Hubert Kurzweil, Ted Oliver. I am very grateful to Fiona Powrie (Garden Curator, Kirstenbosch) who allowed me access to cultivated species of the Bruniaceae in the nursery of the Garden and to Dr. Charles Boucher (University of Stellenbosch) who provided me with unpublished data.

The field trips would not have been successful without the competent guidance of Dr. Dave Macdonald (National Botanic Institute, Kirstenbosch) and Colin Paterson-Jones to the Grootvadersbos Nature Reserve, of Brenda Szabo (National Botanic Garden, Kirstenbosch) to the mountain area above Betty´s Bay and to the Vogelkat Nature Reserve, and especially of the grand old lady of the mountain fynbos, Elsie Esterhuysen, who showed me many rare species in the Hottentot Holland Mountains. Numerous field trips were faciliated by the following forest managers who made a jeep and guides available to me: Chris Martins (Grootvadersbos Forest Station), Mark Johns (Kogelberg Nature Reserve), Dave Osborne (Ladysmith Forest Station) and Leon Lawrence (Hottentotts Holland Nature Reserve). To all of them my deepest thanks.

My thanks are also due to the heads and staff members of the Bolus Herbarium Cape Town, the Herbarium Berlin-Dahlem, the Botanische Staatssammlung München and the Kew Herbarium for providing working facilities at their institutions and for the loan of herbarium specimens.

The second problem has been the interpretation of my findings. When I walked through the Jonkershoek area with Elsie Esterhuysen in 1987 we stopped at a *Nebelia fragarioides* population and Elsie stated that "it is terrible with the Bruniaceae, you never know whether a shoot will flower or not". At that time I thought it might be predictible, but today I know that Elsie was right. To master the enormous variability within the flowering shoot systems of the Bruniaceae it was necessary to reflect upon the Trollian concept of synflorescences and other morphological theories. Finally, the `brunioid´ reference system was created. For stimulating discussions on inflorescence morphology I thank Prof. Dr. Hans A. Froebe (Aachen), Prof. Dr. Focko Weberling (Ulm), Prof. Dr. Anton Weber (Wien), Prof. Dr. Eckehart Jäger (Halle) and Dr. Peter Gleißner (Aachen).

The present work would have been impossible without the financial support of the Deutsche Forschungsgemeinschaft which granted a Habilitationsstipendium for three years (Cl 81/4-1, Cl 81/4-2) and funded three trips to the Cape Province (Cl 81/2-3, Cl 81/6-1).

I am very grateful to the editor of *Opera Botanica Belgica*, Prof. Dr. E. Robbrecht (National Botanic Garden of Belgium, Meise), who enabled me to publish my studies in such an extensive way. For two reasons we intentionally decided for the broad version: (1) The branching patterns in Bruniaceae are so divers that each schematic generalization would inevitably anticipate a certain interpretation. It, thus, appeared reasonable to illustrate each species by at least one profile and in cases of high variation and different ages even by several profiles. Many photographs from living plants and localities were added to complete the presentation. (2) As no morphological concept was found to be adequate to interpret the findings, a new `brunioid´ reference framework was introduced (Claßen-Bockhoff 1994, 1995a,b). It immediately provoked controversial discussions ranging from refusal to acceptance. I got the impression that a historical survey on morphological concepts, terms, and disputes could help to make me understood and the proposed framework acceptable as basis for further discussions. For that reason I included a general chapter on inflorescences in woody plants and a more comprehensive explanation of

the `brunioid´ reference system in the English version. Considering the size of the book, each of the three main chapters are to be read separately.

I also thank Mrs. Marianne Allard (National Botanic Garden of Belgium, Meise) for technical support in course of publication and Mrs. Diplom-Biologist Nancy Kapuskar (Universität Mainz) for reading over the last part of the manuscript. Special thanks are due to Gillian Scott (Constanzia, South Africa), who corrected the grammar and made many stylistic suggestions and to Prof. Dr. E. Jäger who critically commented on the manuscript and recommended it for publication.

When I studied the Bruniaceae my daughter Katrin was an infant and I worked predominantly at home. It was not always easy to manage both, family and research. Without the loving support of my husband Engelbert who always promoted my studies I would never have succeeded. I also warmly thank my mother Anneliese Claßen and Mrs. Emmi Sebastian who have both cared for Katrin in such an affectionate way that I never had to worry about her. To all of them the present book is dedicated.

Summary

The Bruniaceae, which are with one exception endemic to the Cape Floral Kingdom, are one of the most characteristic shrubby elements of the mediterranean fynbos vegetation. Current knowledge of the Bruniaceae is incomplete and neither the infrageneric relationships within the family nor its systematic position within the Angiosperms are clear. The present study has yielded new morphological data concerning the structure and position of the inflorescences of 64 species (ca. 82%).

Both structure and position of the inflorescences are highly diverse within the Bruniaceae. In order to compare the flowering branches of different species in a meaningful way, a new reference system is proposed. It is discussed in terms of current concepts of inflorescence and growth form morphology (e.g. `synflorescences´ sensu Troll, `uni-´ and `conflorescences´ sensu Briggs & Johnson, architectural models sensu Hallé et al.).

The reference system (RS) is defined as a flowering prospectively woody shoot system which coincides with an unit of organization (sympodial unit in case of Bruniaceae) and an unit of time (seasonal growth unit in case of Bruniaceae). The RS is subdivided into the terminal vegetative or flower-bearing `apical zone´, the subterminal or subfloral `renewal zone´ with the primordia of the predominantly cataleptic renewal shoots and the more or less extended `branching zone´ where sylleptic lateral branches may appear. Lateral flowering branches repeat the zones of the main axis in an abbreviated manner. Each RS bears one to many reproductive units (RU) which are defined as the largest repeated flowering units of strictly caducous nature. In comparing different species of Bruniaceae, the individual RUs are taken as being comparable (morphologoically homologous) to each other. They are characterised by both their short life-time and the lack of any persistent shoot elements.

As far as structure and position of the reproductive units are concerned, the Bruniaceae can be divided into four groups: (1) *Thamnea* and *Mniothamnea* with solitary flowers, terminal on leafy branches, (2) *Audouinia, Tittmannia, Linconia* and *Pseudobaeckea teres* with laterally arranged, bracteate short shoots, (3) *Berzelia, Brunia, Staavia* and part of *Raspalia* with cephaloids and (4) *Nebelia, Pseudobaeckea* except *P. teres*, *Lonchostoma* and part of *Raspalia* with truncate cephaloids.

A new infrafamiliar arrangement of Bruniaceae is proposed, based on the results of this study, together with information from published literature: *Berzelia* and *Raspalia* appear to be `core´ genera, *Pseudobaeckea teres* might be better placed in *Tittmannia* and part of the genus *Brunia* might be better transferred into *Berzelia*.

1

Introduction

1.1 Bruniaceae, a southern family

Bruniaceae is a small southern family comprising 78 currently recognised species in 12 genera. With only one exception, *Raspalia trigyna* from Natal, members of Bruniaceae are endemic to the Cape Floral Kingdom (fig. 1) where they form a characteristic floral element of the fynbos vegetation (fig. 2). Adapted to the mediterranean climate most species grow as 'ericoid' shrubs ranging from prostrate rock-crevice species to erect tree-like plants (fig. 3).

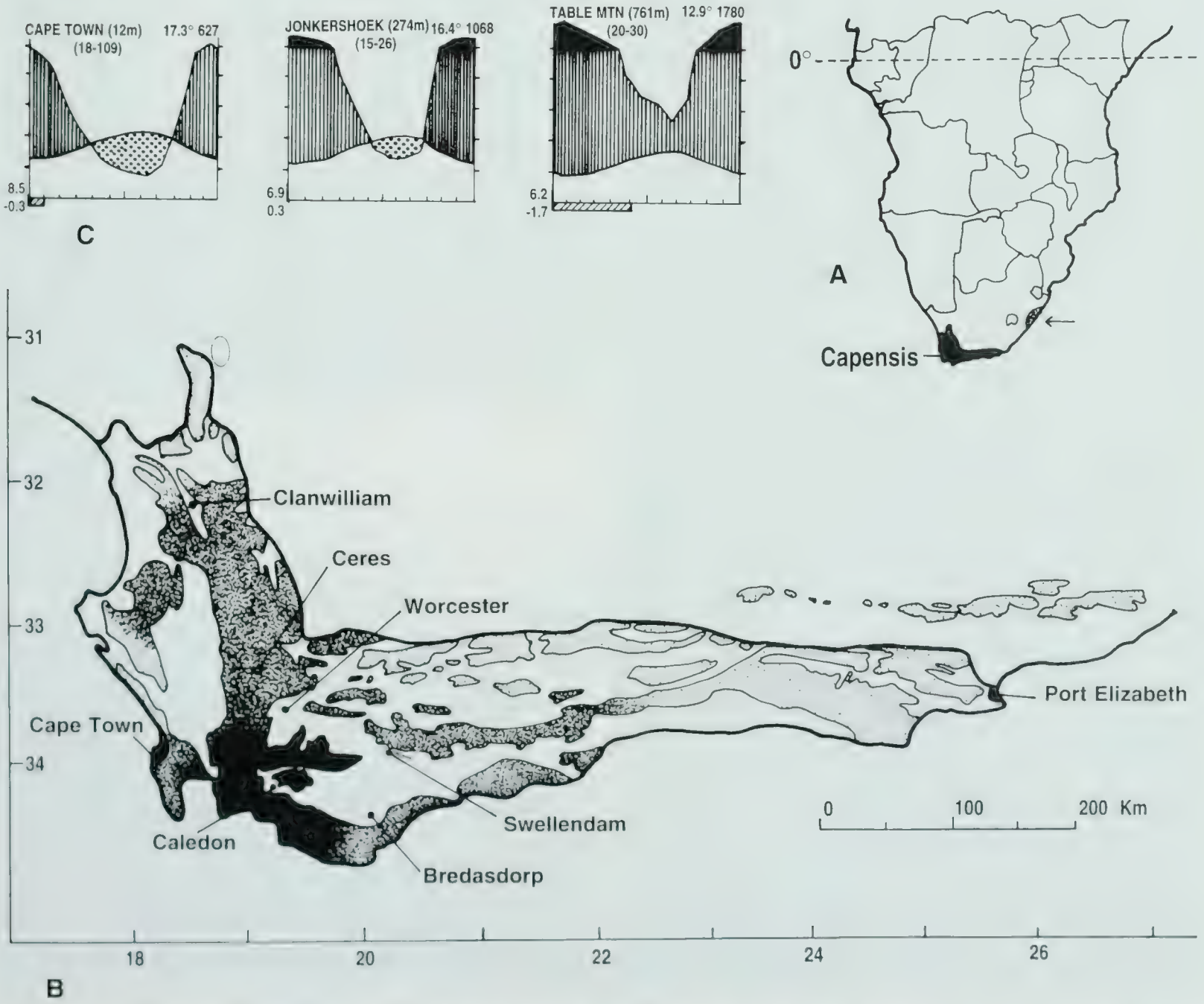


*Figure 1 - **Geographic range of the Bruniaceae in Southern Africa.** The Bruniaceae are endemic to the fynbos vegetation of the Cape Floral Kingdom with only one outlier in Natal (A: arrow). The centre of distribution is the montane fynbos around Caledon (black) where alone 50% of the species occur (B). Many species are only locally abundant, some species are only known from a few populations. Bruniaceae occur predominantly on the south-western slopes of the mountains where the clouds increase humidity (compare with diagrams in C). After Bond & Goldblatt 1984, Walter 1968.*

The Bruniaceae are generally confined to the geological formation known as Table Mountain Sandstone soils of which are characteristically low in nutrients. Several species have lignotubers from which they resprout after periodic fires (fig. 3D). Bruniaceae tend to occur in mesic microhabitats (e.g. southfacing slopes, marshes, streambanks) where they generally grow in isolated patches of a few individuals. Only about a quarter of the species are locally frequent, the remainder being rare and often only known from one or two localities. The red data list of South African plants (Hilton-Taylor 1996) numbers nineteen species as being rare, vulnerable or endangered and four species as being extinct. Hall (1988) found that a quarter of the species have 20% or more (up to 96%) of their pollen grains with irregular appendages, distorted in shape or reduced in size. De Lange et al. (1993a-c) found an extremely low seed to ovule ratio (2,5%) in *Audouinia capitata*. The general picture is that about three-quarters of the Bruniaceae appear to be in a retrogressive, senescent state (Hall 1987a).

Figure 2 - ***Localities of the Bruniaceae****. The Bruniaceae are generally confined to the mediterranean fynbos biome. A, one of the centres of distribution: the Hottentot Holland Mountains near Jonkershoek, B, Proteoid fynbos at the Karbonkelberg with* Staavia radiata *in front, C, Restioid fynbos at Kogelberg Nature Reserve, habitat of* Lonchostoma monogynum, *D, locality of* Staavia glutinosa *on Table Mountain above Nursery Ravine, Kirstenbosch; the top of Table Mountain is completely covered with thick clouds providing the necessary humidity*

The preference of most Bruniaceae for moist sites and the high degree of infertility of *Audouinia* suggest that extant species may be palaeoendemics and that their present distribution dates from the cooler times of the Pleistocene. Hall (1987a, 1988) postulated a great age and a former widespread distribution for Bruniaceous ancestors, only the remnants of which have survived in the climatically and oceanically separated southern tip of Africa. However, there is no indication of where the ancestral stock might have originated, but the remarkably high diversity and the limited geographical range suggest long-term isolation.

*Figure 3 - **Growth habit and reproduction of Bruniaceae**. All species grow as 'ericoid' shrubs mainly of medium size (A), but ranging from prostrate rock-crevice species (B) to erect tree-like plants (C). Dependent on the presence of a lignotuber the Bruniaceae are either reseeders (C) or resprouters (D). A,* Staavia dodii *at Olifantsbos, Cape Peninsula Nature Reserve, about 50 cm in height, B,* Pseudobaeckea teres *at top of Elandsberg, Ladismith, (20 cm high), C,* Berzelia lanuginosa *at Grootvadersbos Nature Reserve: an old* Berzelia *plant more than three metres in height (left) and a field covered with many seedlings (right) after having been burnt some months ago, D,* Tittmannia esterhuyseniae *at 'High Noon', Kaaimansgat: new shoots are sprouting from the lignotuber round the old subterranean stem*

1.2 The infrageneric relationships and the systematic position of the Bruniaceae

Based on anther morphology the family was subdivided into the Audouinieae (*Audouinia, Tittmannia, Thamnea*) and the Brunioideae (remaining genera) by Niedenzu & Harms (1930). Since that time the genera have been rearranged several times according to ovary structure and flower position (Pillans 1947, Takhtajan 1987), pollen morphology (Hall 1988) and leaf anatomy (Carlquist 1991).

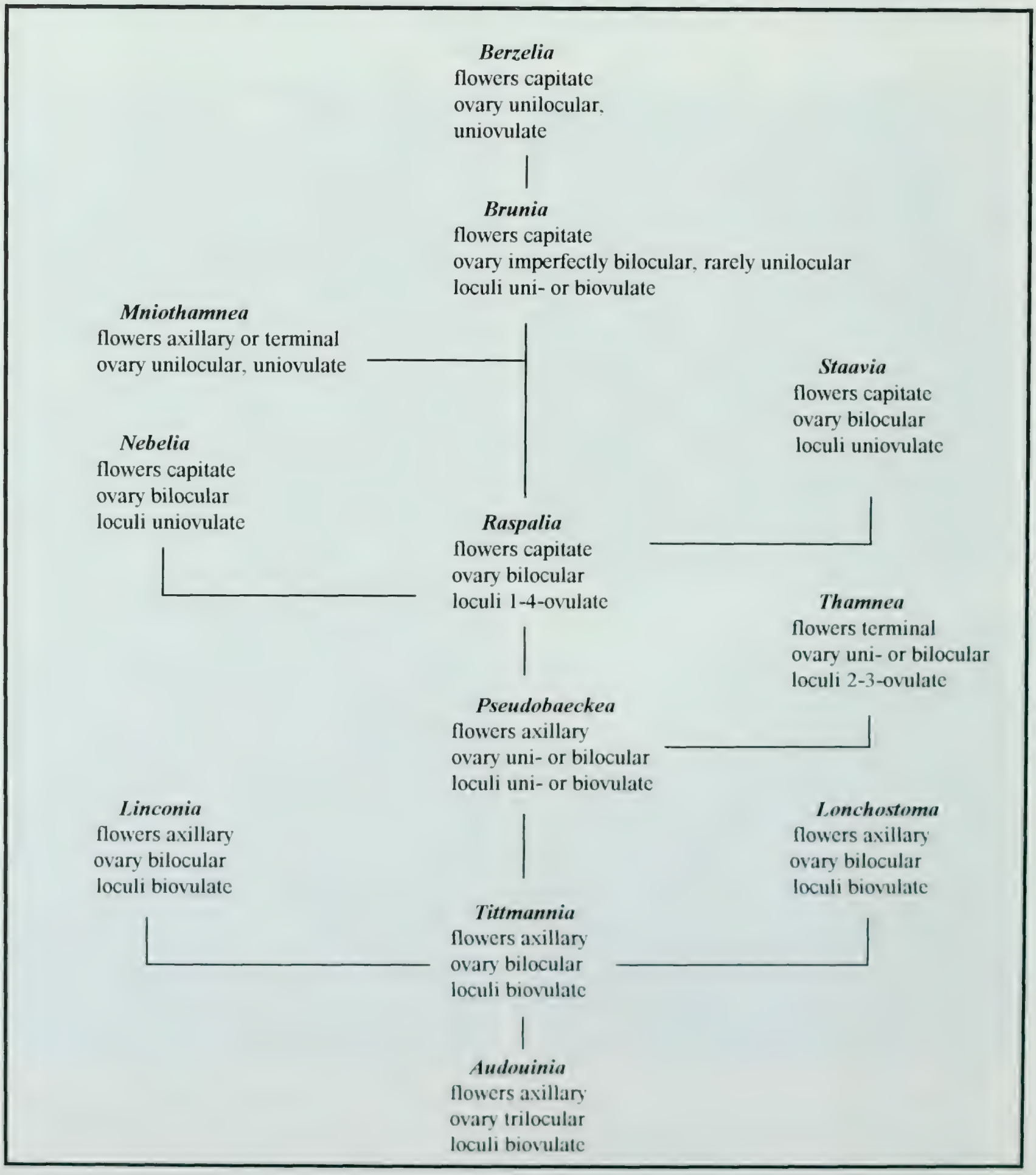


*Figure 4 - **The infrageneric relationships within the Bruniaceae** after Pillans (1947)*

As a general conclusion *Audouinia* is considered to be the most primitive genus with the only palaeodiploid chromosome number and the only trilocular ovary in the family. There is a broad agreement that *Audouinia* is very close to *Tittmannia* and *Thamnea*, but the relationship within the remaining genera is not clear. Pillans (1947; fig. 4) and Takhtajan (1987) consider the uniloculate uniovulate *Berzelia* to be the most advanced genus in the Bruniaceae, but Carlquist (1991) found that *Berzelia* has the same leaf anatomy as *Audouinia*. Altogether the picture seems rather confused (see Claßen-Bockhoff in press).

Dahlgren & Van Wyk (1988), Hall (1988) and Carlquist (1991) have discussed the relationships of Bruniaceae in detail. The most recent concept is that Bruniaceae and the monogeneric Grubbiaceae are closely related, a concept originated by Van Tieghem (1897). Both families widely agree in external morphology, leaf and wood anatomy (Carlquist 1978, 1991), pollen (Hall 1988) and seed morpholgy, embryology and phytochemistry (Dahlgren & Van Wyk 1988), but disagree in phyllotaxis and flower morphology. The systematic position of the two families is not clear.

Since the Bruniaceae were established, the family has generally been placed in widely circumscribed Rosales (e.g. in Hallier 1912, Cronquist 1981), Saxifragales (Takhtajan 1980) or Hamamelidales (Hutchinson 1969). Dahlgren & Van Wyk (1988) follow Cronquist (1988) in placing the Grubbiaceae in Ericales. As a provisional alternative to the above concepts they treat both families, Bruniaceae and Grubbiaceae, in a separate order, Bruniales, near Ericales. In contrast to them Thorne (1976, 1983) placed them in Pittosporales suborder Bruniineae together with the four monogeneric families Geissolomaceae, Myrothamnaceae, Roridulaceae and Hydrostachyaceae, all native to South Africa. This order is associated with the `lower´ Rosidae and is considered to be allied to the Hamamelidaceae. The leaf and wood anatomical data of Carlquist (1978, 1991) widely support Thorne's concept, while embryological data suggest adoption of the concept of Dahlgren & Van Wyk (1988). The first molecular data from *Berzelia* and *Brunia* indicate a position within the Dipsacales - Asterales s.l. - Apiales-group (Olmstead et al. 1993, Backlund et al. 1996).

2

Material and methods

2.1 Material

The study was carried out of the inflorescence morphology of 63 species of Bruniaceae (ca. 82%); fresh material collected by the author was available for 33 species, while herbarium material was used for the remainder.

As far as possible branching patterns of whole plants were examined in the field, the plants and their localities were photographed and shoot apices, flowers and inflorescences of different ages were fixed in 70% alcohol. Vouchers were deposited at the Herbarium of the author (abbreviated as: CLA), the Bolus Herbarium at Cape Town University (BOL) and the Compton Herbarium at Kirstenbosch (NBG).

All specimens of Bruniaceae held at the Botanisches Museum Berlin-Dahlem (B), the Bolus Herbarium Cape Town (BOL) and the Compton Herbarium Kirstenbosch (NBG) were studied. Some specimens from the Botanische Staatssammlung München (M) and the Herbarium Kewensis (K) were included in the study. The species' names have been controlled using the key of Pillans (1947) with some corrections.

The species examined in detail are listed below in alphabetical order following the nomenclature of Hall (1987b).

Audouinia Brongn.

A. capitata (L.) Brongn.: Claßen & Froebe 1271, CLA (fig. 7A, 8A); Claßen-Bockhoff 4000, CLA (fig. 11C); Compton 8916, NBG (fig. 6, 7B); Drège 1853, B (fig. 8B); Ecklon & Zeyher (1914) s.n., B; Garside 4710, B (fig. 8C,D); H.G. 1085, B; Krause 11777, B; Spruner s.n., B.

Berzelia Brongn.

B. abrotanoides (L.) Brongn.: Baschant s.n., B; Claßen 1545, CLA; Claßen & Froebe 1290, BOL (fig. 36C, 38), 1307, CLA (fig. 39), 1381, BOL & CLA (fig. 37, 40); Compton 4469, 13879, 18819, NBG; Garcke s.n., B; Garside 146, B; H.G. s.n., B; Roth s.n., B; Schlechter 428, 9365, B; Walter s.n., B.

B. arachnoidea (Wendl.) Eckl. & Zeyh.: Claßen & Esterhuysen 1410, BOL & CLA (fig. 28A, 29, 30); Claßen-Bockhoff 4006, CLA (fig. 28B); Rourke 824, NBG; Schlechter 8926, B; Taylor 5013, NBG.

B. burchellii Duemmer: Claßen-Bockhoff 4005, BOL, CLA (fig. 24) & NBG.

B. commutata Sond.: Barker 591, NBG; Engler s.n., B (fig. 20, 35A); H.G. s.n., B.

B. ecklonii Pillans: Compton 16527, NBG (fig. 48B); Rourke 983, B (fig. 35B, 48A).

B galpinii Pillans: Claßen & Froebe 1320, 1518, CLA (fig. 43C, 45), 1521, BOL & CLA (fig. 44); Powrie 153, B (fig. 43A,B).

B. incurva Pillans: Williams 2269, NBG (fig. 34, 35D).

B intermedia (Dietr) Schlechtd.: Claßen & Esterhuysen 1420, CLA; Claßen-Bockhoff 4022, CLA (fig. 22) & NBG; H.G. s.n., B (fig. 23, 35C); Stokoe s.n., NBG.

B. lanuginosa (L.) Brongn.: Baschant s.n., B; Bayliss 1636, B; Claßen & Froebe, 1291, 1346, 1371, CLA (fig. 18), 1089, CLA (fig. 13, 17), 1457, BOL (fig. 19); Claßen-Bockhoff 4013, CLA; Drège s.n., B; H.G. s.n., B; Schlechter 8606, B; Walter s.n., B; Werdermann & Oberdieck 50, B.

B. rubra Schlechtd.: Claßen & Esterhuysen 1530, BOL & CLA (fig. 31B-D, 32, 33); Esterhuysen 31690, NBG; Williams 2174, NBG.
B. spec.: Claßen-Bockhoff 4023, CLA (fig. 26, 27).

Brunia Lam.
B. albiflora Phill.: Claßen & Froebe 1519, CLA (fig. 64), 1086, 1520, BOL & CLA (fig. 65); Hort. Kirstenbosch s.n., NBG; Marloth 8377, B.
B. alopecuroides Thunb.: Bean 694, BOL; Carlquist 4978, B; Claßen & Froebe 1363, CLA (fig. 70, 71C, 72, 73), 1364, BOL & CLA; Werdermann & Oberdieck 214, B (fig. 55D); Williams 2073, NBG.
B. laevis Thunb.: Burman 1278, BOL (fig. 60B); Claßen 1542, BOL & CLA (fig. 59, 60A); Claßen & Froebe 1368, BOL & CLA; ex Herb. Engler s.n., B (fig. 60D); H.G. s.n., B; Mathews 34, NBG (fig. 60C); Williams 2274, NBG.
B. macrocephala Willd.: Bolus 6364, BOL (fig. 61C-E); Esterhuysen 10352, BOL, 34763, BOL (fig. 61B), 30223, NBG; Schlechter 2283 , B (fig. 55C, 61A).
B. neglecta Schltr.: Claßen & Froebe 1373, CLA (fig. 56); Esterhuysen 4959, BOL & NBG (fig. 57C), 34932a, BOL (fig. 57B), 35382, BOL; Schlechter 7297, B (fig. 55B, 57A,A′).
B. nodiflora L.: Bayliss 270, B (fig. 55A); Bos 1360, B; Claßen & Esterhuysen 1409a, CLA (fig. 51A, 54); Claßen & Froebe 1265, BOL & CLA (fig. 53); Claßen-Bockhoff 4019, CLA; Drège s.n., B; ex Herb. Engler s.n., B; Esterhuysen 11597, 12829, 25765a BOL (fig. 52); Garside 144, 1400, B; Humbert 9394, B; Rycroft 2226, 3187 NBG.
B. stokoei Phill.: Burman 1279, BOL (fig. 68D); Claßen-Bockhoff 4009, CLA (fig. 69A) & NBG, 4014, CLA fig. 69B); Hort. Kirstenbosch s.n., NBG (fig. 68A,B); M.R.L. 5394, BOL (fig. 68C).

Linconia L.
L. alopecuroidea L.: Ecklon s.n., B; H.G. s.n., B (fig. 79D,E); Martens s.n. (1826), B (fig. 79C); Wurts 402, NBG (fig. 77A, 79A,B).
L. cuspidata (Thunb.) Schwartz: Stokoe s.n., NBG (fig. 77B, 78A,B); Schlechter 9273, B (fig. 77C,D, 78C,D).

Lonchostoma Wikstr.
L. esterhuyseniae Strid: Esterhuysen 31811, BOL (fig. 88C-C′′); Powrie 108, B (fig. 87).
L. monogynum (Vahl) Pillans: Claßen-Bockhoff 4007, CLA, 4015 BOL, CLA & NBG (fig. 2C), Claßen & Esterhuysen 1408, CLA (fig. 88B); Compton, 4120, BOL; Drège s.n., B; Esterhuysen 15789, BOL (fig. 83C, 85); Snijman 53, NBG; Stokoe 56805, NBG.
L. myrtoides (Vahl) Pillans: Compton 11988, NBG, 16225, BOL (fig. 83A, 84A,A′).
L. pentandrum (Thunb.) Pillans: Claßen-Bockhoff 4008, CLA (fig. 82); Compton 18801, NBG (fig 83B, 84B-B′′′); Esterhuysen 13084, 33012, BOL (fig. 84B-B′′′).
L. purpureum Pillans: Goldblatt 1646, NBG (fig. 83D, 86, 88A); Stokoe 6018, BOL, Powrie 4,B

Mniothamnea Niedenzu
M. bullata Schltr Carlquist 4715, B (fig. 94, 95B); Claßen-Bockhoff 4017, CLA (fig 91, 92), 4018, BOL, CLA & NBG; Rourke 638, NBG (fig. 93, 95A); Schlechter 2097, B.
M. callunoides (Oliv.) Niedenzu: Burchell 7079, B, Rourke 1289, NBG (fig 95C,D, 96, 97), Schlechter 2040, B.

Nebelia Neck. ex Sweet
N. fragarioides (Willd.) Kuntze Claßen & Esterhuysen 1406, BOL (fig 103), 1412, BOL & CLA (fig 101, 107A), Claßen & Froebe 1350, BOL & CLA (fig 102, 104, 105), Claßen-Bockhoff 4012, CLA; Drège s.n., B; H.G. s.n., B; Schlechter 9228, B; Werdermann & Oberdieck 209, B
N. laevis (E. Mey.) Kuntze: Drège s.n., B (fig. 111A); M.R.C. s.n., B (fig. 110B); M.R.L. 5467, BOL; Rourke 709, NBG (fig. 107D, 110A, 111B)

N. paleacea (Berg.) Sweet: Carlquist 4780, B; Claßen & Esterhuysen 1409b, 1531, CLA (fig. 96); Claßen & Froebe 1345, 1403 CLA (fig. 115); Drège s.n., B; Esterhuysen 33376, M; Garside 1397, B; Schlechter 5428, B.

N. sphaerocephala (Sond.) Kuntze: Claßen & Esterhuysen 1405, CLA; Drège s.n., B; Esterhuysen 9671, BOL (fig. 109B); Rourke 1049, NBG (fig. 107, 108, 109A).

N. stokoei Pillans: Esterhuysen 30824a, 33362 BOL (fig. 106, 107B), BOL.

Pseudobaeckea Niedenzu

P. africana (Burm. F.) Pillans: Carlquist 4784, B; Claßen-Bockhoff 4004, CLA (fig. 125B); Compton 13538, NBG; Drège s.n., B (fig. 126); Drège 3057, B; Hutchinson 422, BOL (fig. 127B); M.R.L. 9331, BOL (fig. 127A; Rourke 1249, NBG; Rycroft 1367, NBG; ex Herb. Willd. s.n., B.

P. cordata (Burm. F.) Niedenzu: Claßen & Esterhuysen 1411, BOL & CLA (fig. 119-125A); Drège s.n.(H.G.), B; Drège s.n., B; ex Herb. Engler s.n., B; Schlechter 1716, B; Z 2225, B.

P. teres (Oliv.) Duemmer: Burchell s.n., B (fig. 129, 130); Claßen-Bockhoff 4020, BOL, CLA & NBG (fig. 3B, 128, 131); Esterhuysen 33463, B & BOL.

Raspalia Brongn.

R. angulata (Sond.) Niedenzu: Drège s.n., B (fig. 152B,B´); Kies s.n., NBG (fig. 144C, 152A).

R. globosa (Lam.) Pillans: Claßen & Esterhuysen 1533, BOL & CLA (fig. 133-135); Rourke 1319, NBG; Snijman 61, NBG.

R. microphylla (Thunb.) Brongn.: Bos 649, B; Carlquist 4811, 5012, B; Claßen & Esterhuysen 1404, CLA, 1532, BOL & CLA (fig. 145A, 147-150); Claßen-Bockhoff 4011, CLA; Drège s.n., B; Drège s.n., B; Ecklon s.n., B; Mac Pherson s.n., 17, NBG; Schlechter 7270, B.

R. phylicoides (Thunb.) Arn.: Bond s.n., NBG (fig. 144D, 153).

R. sacculata (H.Bol. ex Kirchner) Pillans: Claßen & Esterhuysen 1407, CLA; Esterhuysen 17781, NBG, 26512, B (fig. 136B, 138).

R. schlechteri Duemmer: Schlechter 1750, B (fig. 154).

R. staavioides (Sond.) Pillans: Drège s.n., B; Powrie 136, NBG (fig. 136A, 137)

R. stokoei Pillans.: Carlquist 5053, B (fig. 136D, 140); Esterhuysen 29924, B.

R. trigyna (Schltr.) Duemmer: Bachmann s.n., B (fig. 156); Taylor 2636, NBG (fig. 155); Wood 3029, B.

R. variabilis Pillans: Rourke 711, B (fig. 144B) & NBG (fig. 151).

R. villosa Presl: Drège s.n., B; Esterhuysen 7376, NBG (fig. 136C, 139B); Stokoe 56824, B (fig. 139A).

R. virgata (Brongn.) Pillans: Claßen-Bockhoff 4002, CLA, 4016, CLA (fig. 141) & NBG; Herb. Lübeck s.n., B (fig. 143A); Powrie 33, B (fig. 142, 144A); Schlechter s.n., B (fig. 143B,C); Sonder 2652, B; Stokoe s.n. (26.9.1943), NBG.

Staavia Dahl

S. capitella (Thunb.) Sond.: Burchell 7634, B; Esterhuysen 15617, NBG; Ecklon & Zeyher s.n., B; Goldblatt 1813, NBG (fig. 172, 173A); Schlechter 9842, B; Zeyher s.n., B.

S. dodii H. Bol.: Brunnthaler 493, W; Claßen & Froebe 1321, CLA (fig. 3A, 159-161C, 176); Compton 14554, NBG; Goldblatt 1791, NBG; Wolley 2641, B.

S. dregeana Presl: Claßen-Bockhoff 4001, CLA. (fig. 169, 170); Compton 6348, NBG (fig. 171).

S. glutinosa (Berg.) Dahl: Baschant s.n., B; Bodenstein 164, NBG; Claßen & Froebe 1094, BOL & CLA (fig. 162, 164-166); Claßen-Bockhoff 4023, NBG (fig. 177), 4024, CLA; Drège 1827, s.n. (41), s.n. (351), B; Esterhuysen 32145, M, 35431, NBG; Garside 1326, B; H.G. s.n. (27.10.16), B.

S. radiata (L.) Dahl: Baschant s.n., B; Bayliss 8553, B; Bornträger s.n. (28.7.79), B; Carlquist s.n. (2.10.73), B; Claßen 1540, BOL & CLA (fig. 167B); Claßen & Froebe 1264, BOL & CLA (fig. 167A); Drège s.n., B; ; Garside 4437, 145, B (fig. 173B); Lichtenstein s.n., B; Walter s.n., B; Werdermann & Oberdieck 332, B.
S. verticillata (L.F.) Pillans: Drège s.n., B: Esterhuysen 35268, NBG (fig. 173D, 175).
S. zeyheri Sond.: Goldmann 2061, K (fig. 174A); Powrie 75, B; Williams 752, NBG (fig. 173C, 174B).

Thamnea Soland. ex Brongn.
T. diosmoides Oliv.: Carlquist 4665, B (fig. 184A); Compton 22901, NBG (fig. 185A,A´,C); Schlechter 1662, B (fig. 185B).
T. gracilis Oliv.: Burchell 7342, B (fig. 187).
T. hirtella Oliv.: Esterhuysen 25765, B (fig. 184B, 186B,B´); Rycroft 2711, NBG (fig. 186A,A´).
T. massoniana Duemmer: Claßen & Esterhuysen 1418, BOL & CLA (fig. 182B, 183A-A´´); Claßen-Bockhoff 4010, CLA (fig. 182A); Rourke 1047, NBG (fig. 183B).
T. thesioides Duemmer: Esterhuysen 35408, NBG (fig. 184D, 188A,A´), 35105, B; Schlechter 419, B (fig. 184C, 188B,B´).

Tittmannia Brongn.
T. esterhuyseniae Powrie: Claßen & Esterhuysen 1527, BOL & CLA (fig. 191B,D, 192, 193, 195); Claßen-Bockhoff & Esterhuysen 4021, BOL, CLA & NBG (fig. 3D, 191A,C); Esterhuysen 32117, NBG, B.
T. laevis Pillans: Carlquist 4850, B; Esterhuysen 17780, NBG (fig. 199).
T. laxa (Thunb.) Presl: Baschant s.n., B; Bodkin 1153, B; Carlquist 5051, B; Compton, 16093, NBG (fig. 196A, 198); Drège s.n., B; Esterhuysen 28625, B (fig. 196B, 197); Schlechter 8874, B; Williams 2038, NBG.

2.2 Methods

2.2.1 Procedure

The branching patterns were studied in the fresh or dry condition. In some cases it was necessary to analyze fixed and soaked material (70% alcohol). A binocular with drawing-mirror (WILD 113 type 308700) and a two-armed cold lighting (SCHOTT) were used.

Sections from the flowering tops of adult shrubs constituted most of the study material. Only in a few cases was it possible to reconstruct the entire life cycle of a species.

From the material of each species studied, the most characteristic shoot systems were selected and documented by schematic profiles. All drawings correspond in maintaining the relative proportions and in using identical symbols (§ 2.2.4).

For added clarity the foliage in many cases has been omitted. The foliage of the Bruniaceae follows a very dense spiral and often penetrates into the inflorescence. The leaves are small, simple and persistent for several seasons. Within the profiles selected branches show how long the foliage persists. In illustrations of leaf metamorphosis stipules have been mostly omitted.

As species in Bruniaceae have no buds, tegments or cataphylls, no seasonal leaf loss and almost no difference in the length of the internodes, it is not easy to identify the individual seasonal growth units. However, with increasing age the leaves lose their soft hairs and become hard and brownish. In addition, the different life stages of the inflorescences help to reconstruct the age structure of the shoot system. Within the profiles the individual seasonal growth units are separated from each other by an interruption or a different thickness of lines. Very often the relations in time are additionally explained by the legend.

2.2.2 Glossary

The shoot systems examined are treated primarily as vegetative branching patterns with flowers, not as inflorescences. Therefore, the elaborate terminology usually applied to inflorescence morphology is inappropriate. The intention is to describe the shoot systems with very common terms and to introduce only a few new terms. A glossary of the most important terms used in § 3 is given below (see also p.66/67, § 4.1, § 4.3):

cataleptic, catalepsis	lateral shoots arising from their mother axis after at least one resting period are called cataleptic shoots (compare with Müller-Doblies & Weberling 1984)
determinate lateral shoot (dL)	lateral flowering shoots which bear a terminal flower or inflorescence are called determinate
indeterminate lateral shoot (iL)	lateral flowering shoots which bear no terminal flower/inflorescence are called indeterminate; the apex dies off or continues to grow
inflorescence	a mere descriptive term for any flower aggregate
monopodial unit (MU)	one season old part of a monopodial or sympodial shoot system arising terminally from the apex of an older part of the shoot and usually continuing terminal growth in the next season

reference system (RS) — reference unit in order to compare flowering shoot systems of different plants; it is defined as a flowering prospectively woody shoot system which coincides with an unit of organization (sympodial unit in case of Bruniaceae) and an unit of time (seasonal growth unit in case of Bruniaceae). The RS is subdivided into a (non)flowering `apical zone', a subterminal/subfloral `renewal zone' and an (un)branched `branching zone' (see § 4.3.2)

renewal shoot, - zone (R, rz) — applies to the regeneration of perennial plants: after a resting period a shoot system regenerates by reactivating the apex of the main axis (monopodial mode) or by cataleptic lateral shoots called `renewal shoots´ (`Innovationstriebe' sensu Troll 1951) (sympodial mode); the renewal shoots of a woody plant are arranged in a definite subterminal or subfloral zone (renewal zone) of the main axis of the seasonal growth unit and, as far as the lateral branches repeat the zones of the main axis, in further renewal zones of higher orders of branching (rz´, rz´´ ...)

reproductive unit (RU) — reference unit in order to compare inflorescences of different woody plants; it is defined as the largest repeated flowering unit of strictly caducous nature (see § 4.3.3)

seasonal growth unit (SGU) — part of the perennial shoot system which has formed within a single growing season, arising terminally or laterally from an axis formed in a previous growing season (compare with Briggs & Johnson 1979)
(the term is related to the season and not to the year to take the different climatic conditions into consideration; it largely corresponds to the `Schub´ sensu Pilger 1922 and the `unit of extension´ sensu Hallé et al. 1978 extending the latter to sympodial shoot systems)

sylleptic, syllepsis — lateral shoots arising at the same period as their mother axis are called sylleptic shoots (compare with Müller-Doblies & Weberling 1984)
(the term comprises two different kinds of syllepsis: (1) the `normal´ development of sylleptic lateral shoots which, relative to the longitudinal symmetry of the parent shoot, predominantly appear in the medial part of the shoot concerned and (2) the occasional premature growth of the distally arranged, virtually cataleptic renewal shoots)

sympodial unit (SU) — branched or unbranched shoot of limited growth measured from the point of its lateral insertion on the parent axis up to its vegetative or reproductive end (compare with Troll 1954); if perennial, one or several monopodial units are inserted

2.2.3 Abbreviations

The following list summarizes all abbreviations used in the present text. In general shoot and shoot systems are listed in capitals, processes in capitals and italics and all the remaining abbrevations in small letters. To facilitate reading selected abbreviations are also found in the cover of the book. In contrast to the remainders these often repeated abbreviations are not again explained in the legends of the individual figures.

A *Aggregation*
a anthotelic
am amphitony/amphitonic
an anauxotelic
au auxotelic
az apical zone

B *Branching*
ba basitony/basitonic
bi basal internode
bz branching zone

C Conflorescence
C^2 superconflorescence
c cryptocorm
cfL cataleptic flowering Lateral shoot
cfR cataleptic flowering Renewal shoot
cL cataleptic Lateral shoot
Co *increasing Complexity*
coF co-Florescence
cR cataleptic Renewal shoot
cvL cataleptic vegetative Lateral shoot
cvR cataleptic vegetative Renewal shoot

D *Disjunction*
di dense internodes
dL determinate Lateral shoot
Dm *Dimorphism*

e element
ei end-internode
En *Enrichment*
ep epitony/epitonic
ez enrichment zone

F Florescence
f flower
fl flowering
fr fruiting
fz flowering zone

H *Homogenization*
hy hypotony/hypotonic
hyp hypotagma

i inflorescence
I Inflorescence axis
I *Inhibition*
ia aggregate of inflorescences
Iap *Inhibition of apex*
ib inflorescence bud
Iin *Inhibition* of inflorescence
iL indeterminate Lateral shoot
ini intercalary inflorescence
ins innovation shoot
ipi inflorescence primordium inhibited
Irz *Inhibition* of renewal zone
is inflorescence shoot
iz inhibition zone

L Lateral shoot
lb leaf base
li lateral inflorescence
lia lateral aggregate of inflorescences
lfR late flowering Renewal shoot
lJ late Juvenile sprout
lL late Lateral shoot

M Main axis
mc monopodial connection
me mesotony/mesotonic
mF main Florescence
Mg Main axis growing on terminally
MU Monopodial Unit

n growth period, season

o overtopping

P Primary axis
P *Proliferation*
p precipitaton
pc paraclade
pF partial Florescence
Po *Positional change*
pp prophyll
psF pseudo-Florescence

R *Reduction*
R Renewal shoot
rb reproductive bud
Rfo *Reduction* of foliage
RJ Rejuvenative shoot
RL *Reduction* of Lateral shoot
rs repeating shoot
RS Reference System
RU Reproductive Unit
Rz *Razemization*
rz renewal zone
rz-1 renewal zone of the parent axis

S Synflorescence
Sb *Substitution*
sc sympodial connection
se sepal
sfL sylleptic flowering Lateral shoot
sfR sylleptic flowering Renewal shoot
SGU Seasonal Growth Unit
sL sylleptic Lateral shoot
smc sylleptically starting monopodial connection
Sp *Specialization*
sR sylleptic Renewal shoot
st stipule
SU Sympodial Unit
svL sylleptic vegetative Lateral shoot
svR sylleptic vegetative Renewal shoot

$T_{1,2,3}$ *1st, 2nd, 3rd Truncation*
t terminal
Te *Terminalization*
Tf *Transformation*
tf terminal flower
ti terminal inflorescence
tia terminal aggregate of inflorescences
Tm *shifting in Time*
Tp temperature
tz transitional zone

U Uniflorescence
UE Unit of Extension
UF Unité de Floraison
UM Unit of Morphogenesis

vb vegetative bud
vR vegetative Renewal shoot
vs vegetative shoot
vz vegetative zone

wi wide internodes

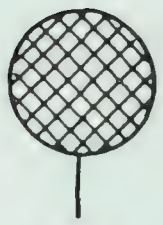
ZE Zuwachseinheit

I,II, .. orders of branches
', ", ... orders of lateral structures/processes
+/- feature strong/weak
(-) missing

2.2.4 Symbols

flower

inflorescence

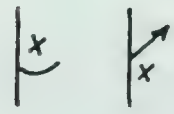


aggregate of inflorescences

flower/inflorescence in bud

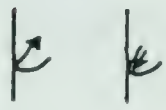
flower/inflorescence deflorated

flowers/fruits fallen off



organs fallen off, missing

node with leaf



node with leaf and axillary bud

shoot with active apical meristem

shoot with inhibited apex

shoot broken off, damaged

shoot in graph interrupted

shoot in graph extended in length

3

Structure and position of the inflorescences

3.1 *Audouinia* Brongn.

The monotypic genus Audouinia *is considered to be the most primitive genus in Bruniaceae (see p.15). The distribution of* A. capitata *is restricted to the Cape Peninsula except for a single known plant near Hermanus, approximately 75 km from the closest population. Altogether 27 populations are known with about 1200 individual plants (De Lange & Boucher 1993b). Hilton-Taylor (1996) categorized the species as 'vulnerable'. As a model to investigate the processes of rarification and extinction of plants in the Western Cape, extensive autecological studies were initiated by the National Botanical Institute (De Lange et al. 1990, 1993a-g, Wright et al. 1991). It was found that the reproductive vigour of the plant was limited by inefficient pollination, a low pollen viability, a very high measure of sexual self-incompatibility, a high incidence of aberrant endosperm development and embryo abortion, poor seed set and high seedling mortality (De Lange & Boucher 1993b). In contrast to its poor sexual reproductive capaciy the plants are able to regenerate successfully from a lignotuber. De Lange & Boucher (1993b) postulated that efficient resprouting ability was the product of greater emphasis on selection for resprouting and longevity than on selection for sexual efficiency. They consider that lignotuber formation is an ancestral trait and obligate seed production an advanced one.*

Figure 5 - **Audouinia capitata**. *A, a potted plant, originally from the Cape Point Nature Reserve, cultivated at the nursery of the National Botanic Garden Kirstenbosch, B, a medium-sized inflorescence in full bloom.*

Growth and branching pattern. *A. capitata* is an erect subshrub, usually 30-50 cm high, with rod-shaped branches (fig. 6). Because of the low reproductive vigour of the species, young plants are only rarely found in nature. Experiments have shown that smoke derived from burning fynbos plant material stimulates germination (De Lange & Boucher 1990). The length of the juvenile phase is unknown. De Lange & Boucher (1993b) demonstrated that a fourteen year old plant of 76 mm height was still in the juvenile phase. They postulated the juvenile phase to be exceptionally protracted, possibly in excess of twenty years.

A. capitata flowers from April to September, that is in the coldest months of the south hemispherean winter. When flowering, the thin shoots are characterized by spicate inflorescences (fig. 5B). Within a SGU the clustered flowers are arranged subterminally (fig. 6). Figure 11B shows that the part of the main axis protruding from the inflorescence has not been formed after flower formation, but before. Thus, the flowers from the beginning appear in a subterminal shoot zone (compare with § 4.3.3.2-3).

Individual SGUs are highly variable. Sylleptic flowering lateral shoots may be present (fig. 7A, 8A,C: sfL) or are missing (fig. 6). Occasionally only lateral inflorescences are formed and the subterminal inflorescence of the main axis is absent (fig. 8A,D). More rarely, sylleptic vegetative lateral shoots (which come to flower in the next season) arise from the middle of the inflorescence (fig. 7A, 8A: svL).

The apex of the main axis may either die off (fig. 8A,B) or continue to grow on vegetatively (fig. 7B, 8A,C,D, 9B: mc). In the first case several lateral shoots are formed above the cluster of flowers, the two or three uppermost functioning as renewal shoots by dominating the remainder (fig. 8A: R, sR). In the latter case monopodial units are formed. Figures 6 and 7B show an individual shoot system with at least two monopodial connections in series. Within such a perennial sympodial unit a clear age gradient is present. The position of the former inflorescences is often recognizable by the spread leaves and occasionally by some persistent flower stalks (fig. 7B: fz). The leaves change their quality with age, being soft and hirsute in the first season (fig. 7B: n), harder and glabrous in the second season (n-1) and sclerophyllous and greyish in the third season when leaf-drop commences (n-2).

*Figure 6 - **Audouinia capitata.** Habit of flowering shoot systems (Compton 8916, NBG) arrows: flowering sequence (compare with fig. 7B).*

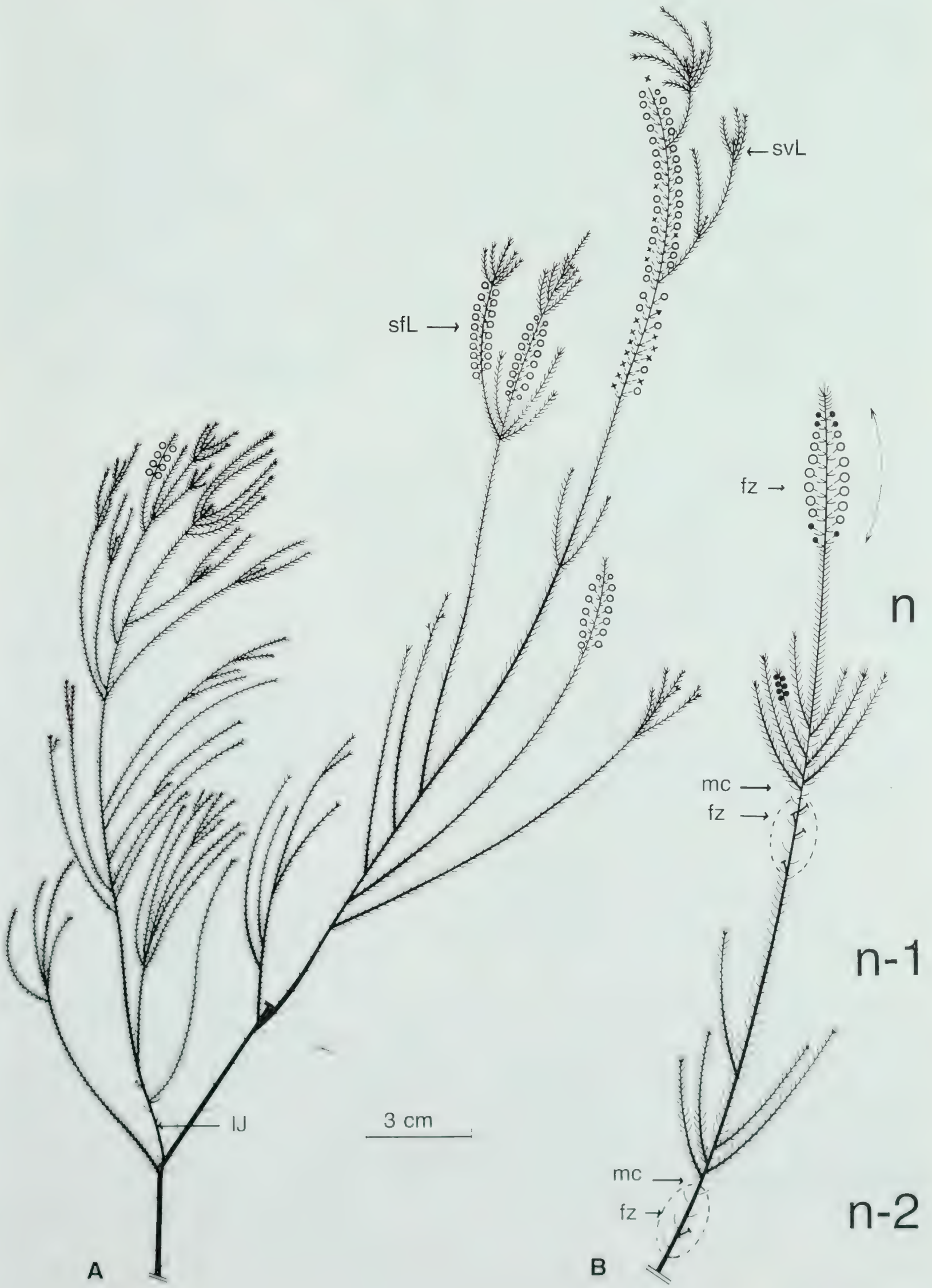


Figure 7 - **Audouinia capitata**. *Profiles of flowering shoot systems.*
lJ, *late juvenile sprout; arrows in B: flowering sequence (compare with fig. 6)*

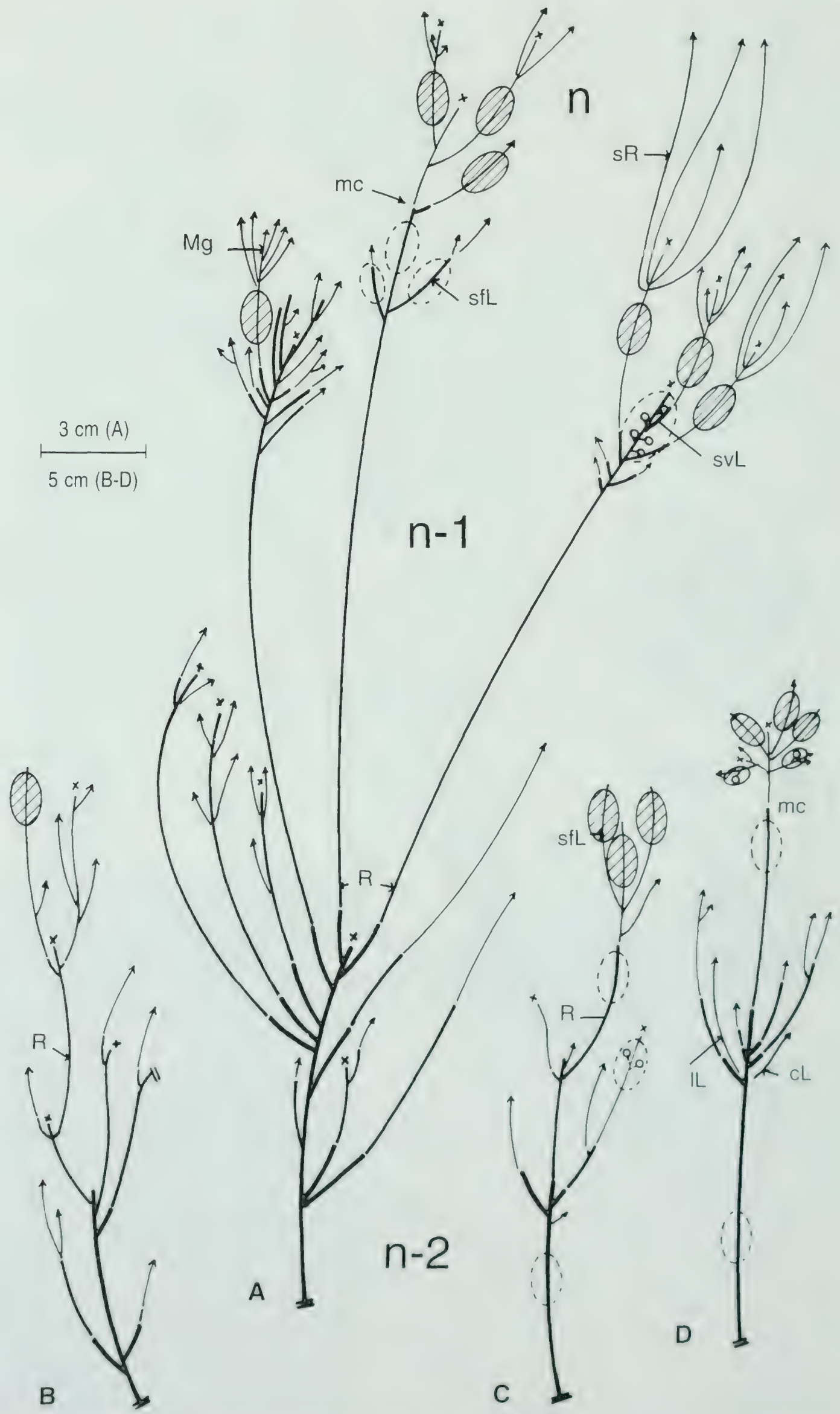


Figure 8 - **Audouinia capitata**. *Profiles of flowering shoot systems*

cL, *cataleptic lateral shoot*, lL, *late lateral shoot*,
Mg, *main axis growing on terminally*, sR, *sylleptric renewal shoot*

Comparing the shoot systems of figure 7A and figures 8B-D and 9A, a high degree of variability is clearly shown. In figure 7A the flowering SGU has a total length of about 27 cm. The very large inflorescence of the dominant shoot is borne terminally in this instance and sylleptic vegetative lateral shoots (svL) are present. A well developed sylleptic flowering lateral shoot system (sfL) is also present. A late juvenile sprout (lJ), much branched and just starting to flower, has arisen from old wood. Following the dates given by De Lange & Boucher (1993b) the shoot system appears to have been stimulated by a recent fire. In contrast, the SGUs shown in the figures 8B-D and 9A appear to be old, almost exhausted branch systems. The total length of the individual SGUs is only about four centimeters, branching is reduced and the inflorescences comprise only a few flowers.

De Lange & Boucher (1993b) found that the vegetative vigour of shoots, the size and number of inflorescences, and seed set were all increased by fire. A regime of late summer burns (January to March) and a fire frequency of about fifteen years may be favourable for *A. capitata*. However the vitality of a given plant depends not only on its relative post-fire age, but on its total age as well. The latter is difficult to reconstruct. Radiocarbon dating of lignotubers indicate an age of approximately ninety years (De Lange & Boucher 1993b), but as fragmentation of the lignotuber can not be excluded, a much greater age of the plants is likely.

Leaf metamorphosis and inflorescence structure. The large inflorescences of conspicuous red flowers (fig. 5B, 11B,C) appear superficially spicate. As Niedenzu & Harms (1930:297) noted however, each of the flowers is surrounded by usually eight (according to personal observation: up to sixteen) bracts which are spirally arranged as is the foliage (fig. 10B-I). As fig. 10 shows, the bracts clearly differ from the leaves being much smaller, thinner and paler than the foliage leaves. The bracts gradually increase in size in a proximal to distal direction and then merge into the calyx (K) also comprising pale ciliate segments. Leaf metamorphosis then becomes abrupt and gives rise to a corolla comprising unguiculate petals of an intense red colour (L).

Besides the presence of a high number of bracts, the flowering sequence contradicts interpretation of the inflorescence as a simple spike. Quite often anthesis begins in the centre of the flower cluster and continues in a divergent way (fig. 6, 7B, 11A). However large inflorescences may occasionally show an acropetal, but discontinuous flowering sequence (fig. 7A, 11C). As the species flowers in winter, climatic factors may influence the total duration and continuation of anthesis. Comparable data are given by De Lange et al. (1993d) who found that receptive flowers on individual plants were present for three weeks up to two months.

The fact that vegetative shoots occasionally arise from the inflorescence constitutes a third reason for not interpreting the inflorescence of *A. capitata* as a simple spike. The inflorescence is clearly a cluster of solitary flowers, each terminating a bracteate short-shoot (fig. 11A), occasionally being separated from the other flowers by numerous bracts and, more rarely, by vegetative shoots.

As De Lange et al. (1993d) have shown, fire clearly stimulates flowering. Flower production was highest during the first post-fire season during which inflorescences up to 150 mm in length and individual plants bearing more than 500 inflorescences (maximum: 822 inflorescences per plant) were found. The average number of inflorescences per plant is twenty-four, the average length of the inflorescences is 20-50 mm and the number of flowers varies from a few to more than one hundred (De Lange et al. 1993d). The flowers are pollinated by small pollen-feeding beetles (Coleoptera: Nitidulidae) which perhaps seek shelter in the florets (Wright et al. 1991, De Lange et al. 1993d). Pollen dispersal by these beetles, however, is limited to short distances (less than four metres), which results in a limited gene flow within *A. capitata* populations.

Figure 9 - **Audouinia capitata.** *Shoot systems of plants cultivated at the nursery of the National Botanic Garden Kirstenbosch. A, flowering shoots in August 1996, B, post-flowering shoots in November 1996 with new vegetative growth.*

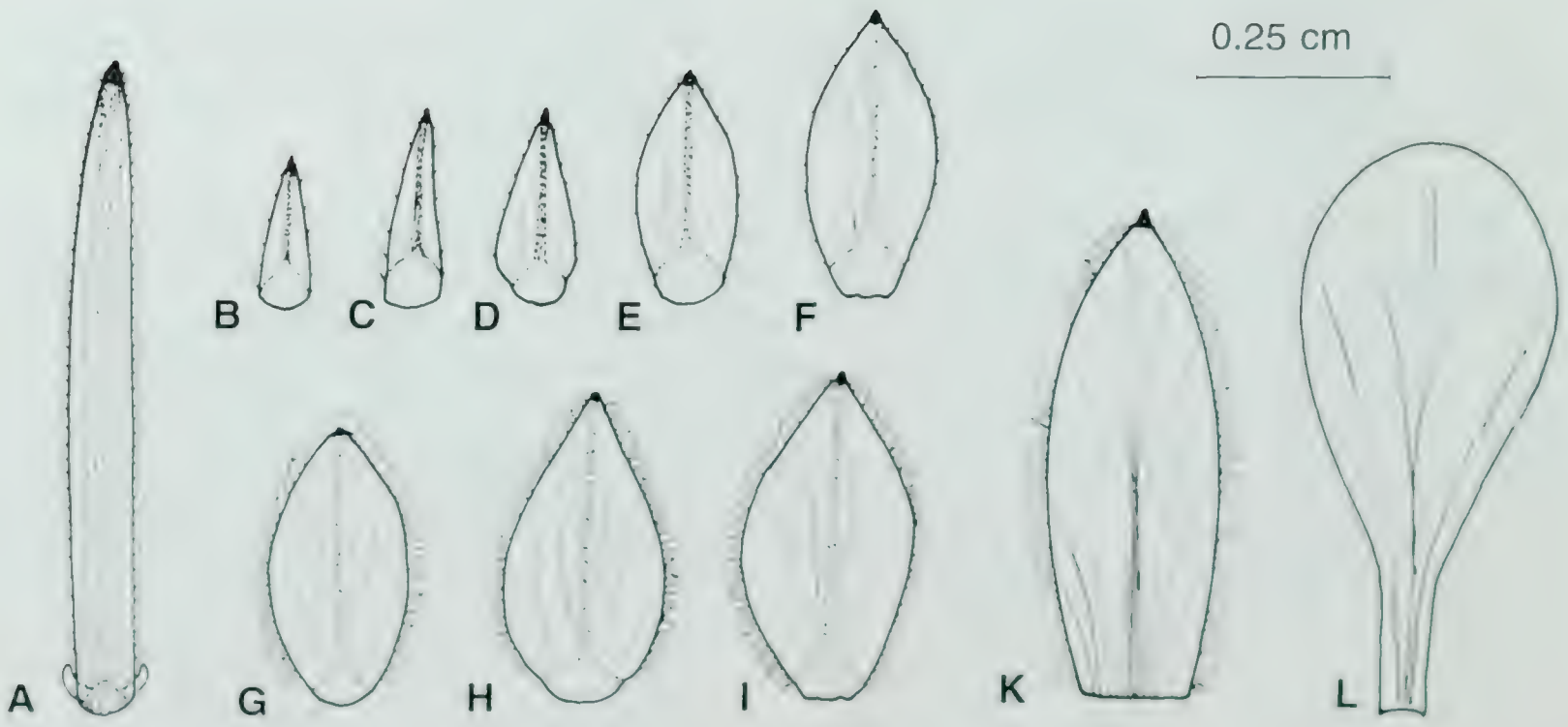


Figure 10 - ***Leaf metamorphosis in*** **Audouinia capitata**. *A, folious leaf with mucronate tip and small stipules, B-J, ciliate bracts surrounding the flower, K, ciliate sepal with black leaf tip, L, petal.*

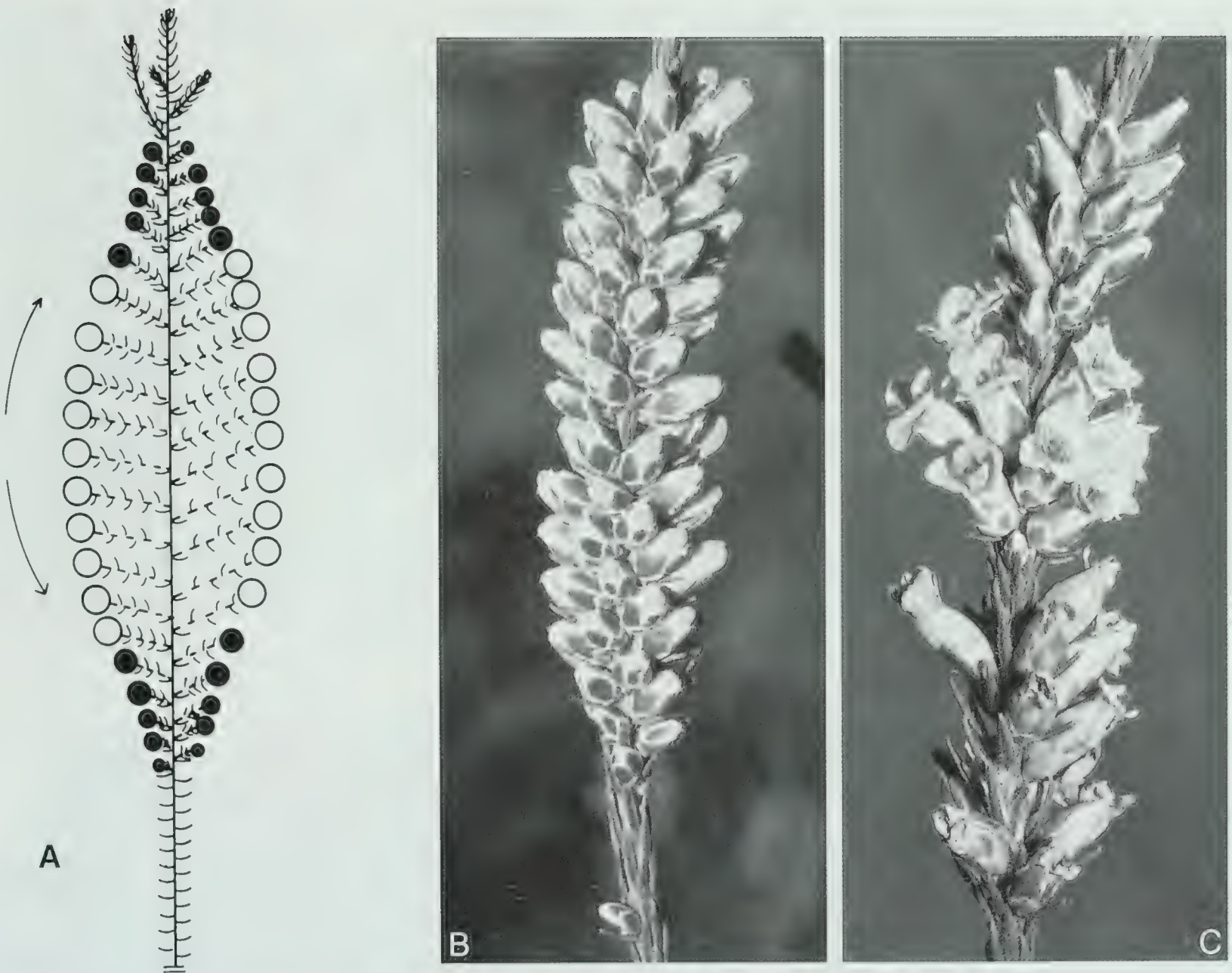


Figure 11 - ***Inflorescences of*** **Audouinia capitata.** *A, profile of an inflorescence showing its subterminal position, the numerous bracts surrounding the individual flowers, the divergent flowering sequence (arrows) and the vegetative shoots above the flower cluster, B, an inflorescence in bud and C, in anthesis showing an acropetal, discontinous flowering sequence.*

Summary. Figure 12 shows the model of the monotypic genus *Audouinia*. In figure 12A the special case of a sympodial unit (SU) developing in exactly one season is presented. In the present study this special case is taken as a reference system (RS) for comparison with all the flowering shoot systems of the different species (compare with § 2.2.2 and 4.3.2).

The RS arises laterally from the renewal zone of its mother axis (rz-1) and shows (from proximal to distal) the branching zone (bz), which is flowering in *Audouinia*, the renewal zone (rz), which is always above the inflorescence in *Audouinia*, and the apical zone (az), which is shown here with an apex dying off to fulfil the definition of the RS as a sympodial unit. With the exception of the flowering short-shoots, all axes are densely covered with foliage.

Figures 12B-D show some variations of the model: the pronounced tendency of the apex to continue its vegetative growth, forming monopodial units (B: mc); the variations of the branching zone in respect of the quantity and nature of the lateral shoots and their time of developing (C: *B*), and the formation of heterogenous inflorescences that incorporate vegetative shoots (D: svL).

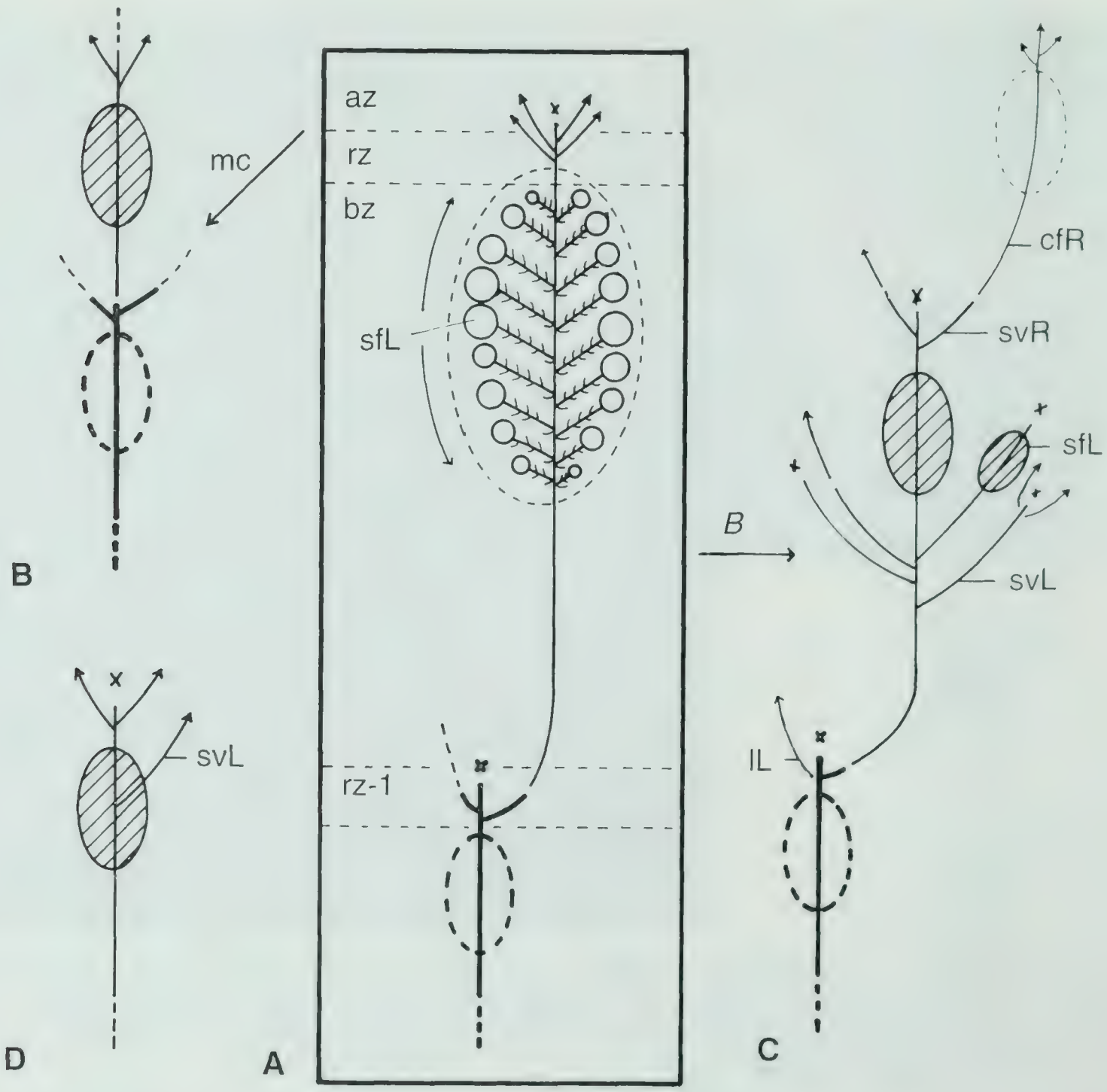


Figure 12 - ***Model of the monotypic genus*** **Audouinia**. *A, model of a flowering shoot that corresponds to both a seasonal growth unit and a sympodial unit: the apex dies off, the renewal zone is always above the subterminal inflorescence, which is a cluster of unifloral bracteate short-shoots. B-D, variations of the model: B, forming of monopodial units, C, variations of the branching zone, D, interruption of the inflorescence by a vegetative shoot.* *B, branching,* lL, *late lateral shoot.*

3.2 ***Berzelia*** Brongn.

Berzelia *(12 species) is the second largest genus of the family. Several species, especially* B. lanuginosa, *are common. As some grow as tall shrubs,* Berzelia*s may be conspicuous elements of a given vegetation (fig. 3C, 13B,C, 21A, 42A).*

Seven species have been studied in the field: B. lanuginosa *at several localities in the Western Cape Province,* B. abrotanoides *in the Cape Point Nature Reserve, near Kleinmond and near Bredasdorp,* B. arachnoidea *and* B. rubra *in the Hottentots Holland Mountains and* B. intermedia, B. galpinii *and* B. burchellii *in the Langeberg-area. With the exception of* B. burchellii *and* B. rubra *the named species, and cuttings of* B. ecklonii, *are cultivated at the National Botanic Garden Kirstenbosch. An indetermined species cultivated at Kirstenbosch has been included in the present study.* B. ecklonii, B. commutata *and* B. incurva *have been analysed from herbarium specimens.*

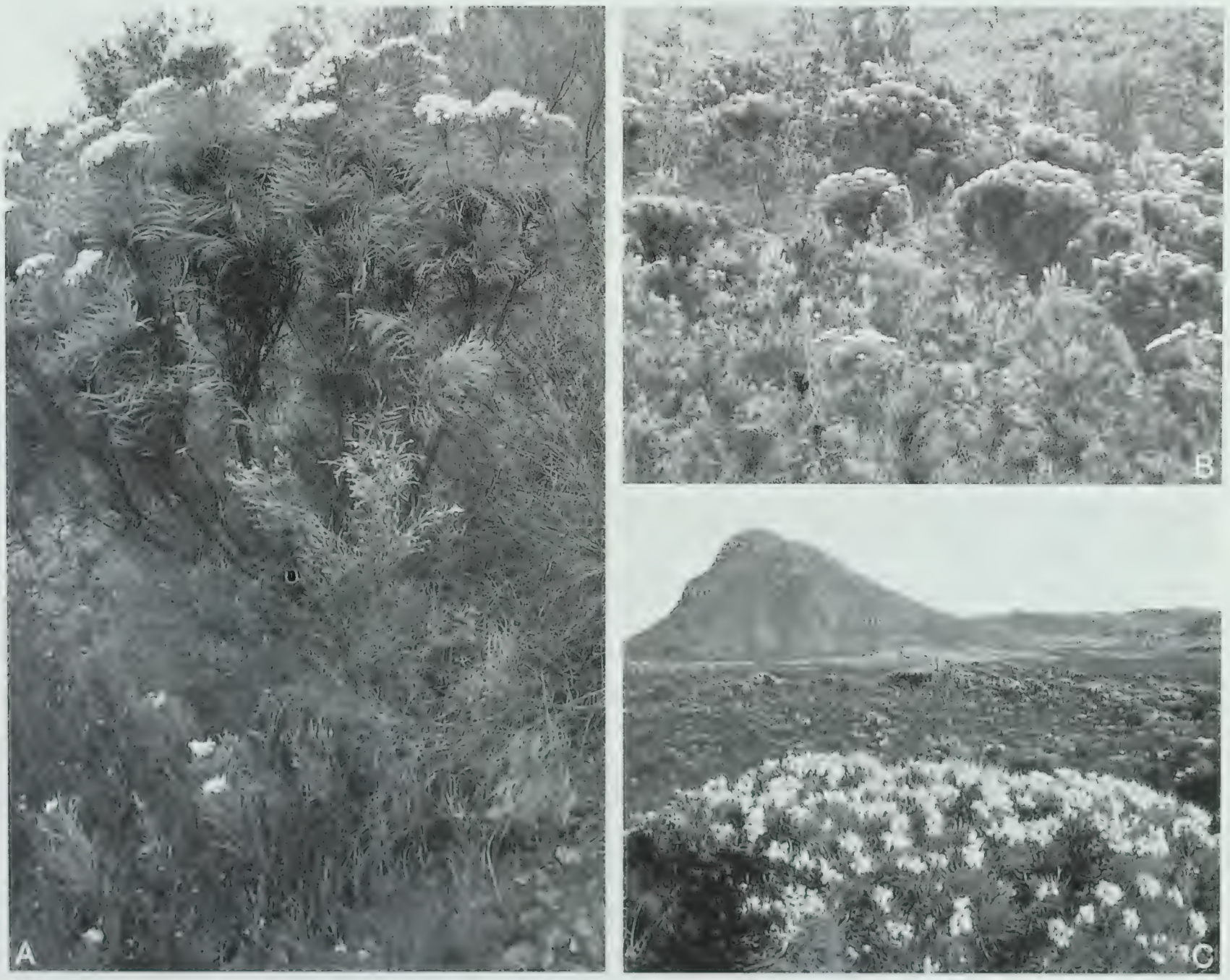


Figure 13 - **Berzelia lanuginosa**. *Habit of flowering plants: A, a plant of about 2,5 m height with seedlings in the foreground at the Contour Path, Kirstenbosch, B, mountain fynbos above Goedehope Farm, Grootvadersbos Nature Reseve, with a large population of erect shrubs, C, coastal fynbos at the Cape Point Nature Reserve with many low shrubs and seedlings.*

Growth and branching pattern. All species are erect shrubs of one to two meters height or more; *B. lanuginosa*, *B. galpinii* and *B. intermedia* may reach a height of four meters. As is the rule with small trees, a dominant stem is often present which in this genus remains relatively thin. The habit, shown in figures 21A, 31B, 36A, 42B,C, shows one or a few thin stems and a heavy, much-branched canopy. This characteristic habit is also found in some other Bruniaceae, e.g. in species of *Brunia* (§ 3.3) and *Staavia* (§ 3.10).

In comparison with the well-studied *Audouinia capitata*, little is known about the biology of *Berzelia*. There is only one phenological study (Le Roux et al. 1984) which deals with the seasonal growth rhythm of *B. lanuginosa* (fig. 14):

After a dormant period of about six months, the apex of the dominant shoot recommences growth in January of season *n*. A sylleptically branched shoot system is formed until the end of June *n*, when the apex suspends its activity until the next season (January *n* + *1*). The SGU of season *n* is thus formed in about six months, being completed in the beginning of July *n*, when the first inflorescences start to flower. The reproductive period from flower bud formation (June *n*) until seed dispersal (May *n* + *1*) lasts for about one year. Anthesis coincides with the wet season which falls in the south hemispherean winter (July-December), while fruit and seed set take place in the following drier months.

Although the fruiting period of season *n* overlaps the next period of vegetative growth (*n* + *1*) in *B. lanuginosa*, both periods, vegetative and reproductive, are more or less clearly separated from each other within an individual SGU. This probably holds for other *Berzelia* species, which show a characteristic subdivision of individual SGUs into a proximal zone bearing vegetative branches and a distal zone bearing inflorescences (e.g. fig. 24, 27, 37, 48). However, vegetative branches occasionally appear within the flowering zone (e.g. fig. 22, 43) and medial branches may flower together with the main axis (fig. 39).

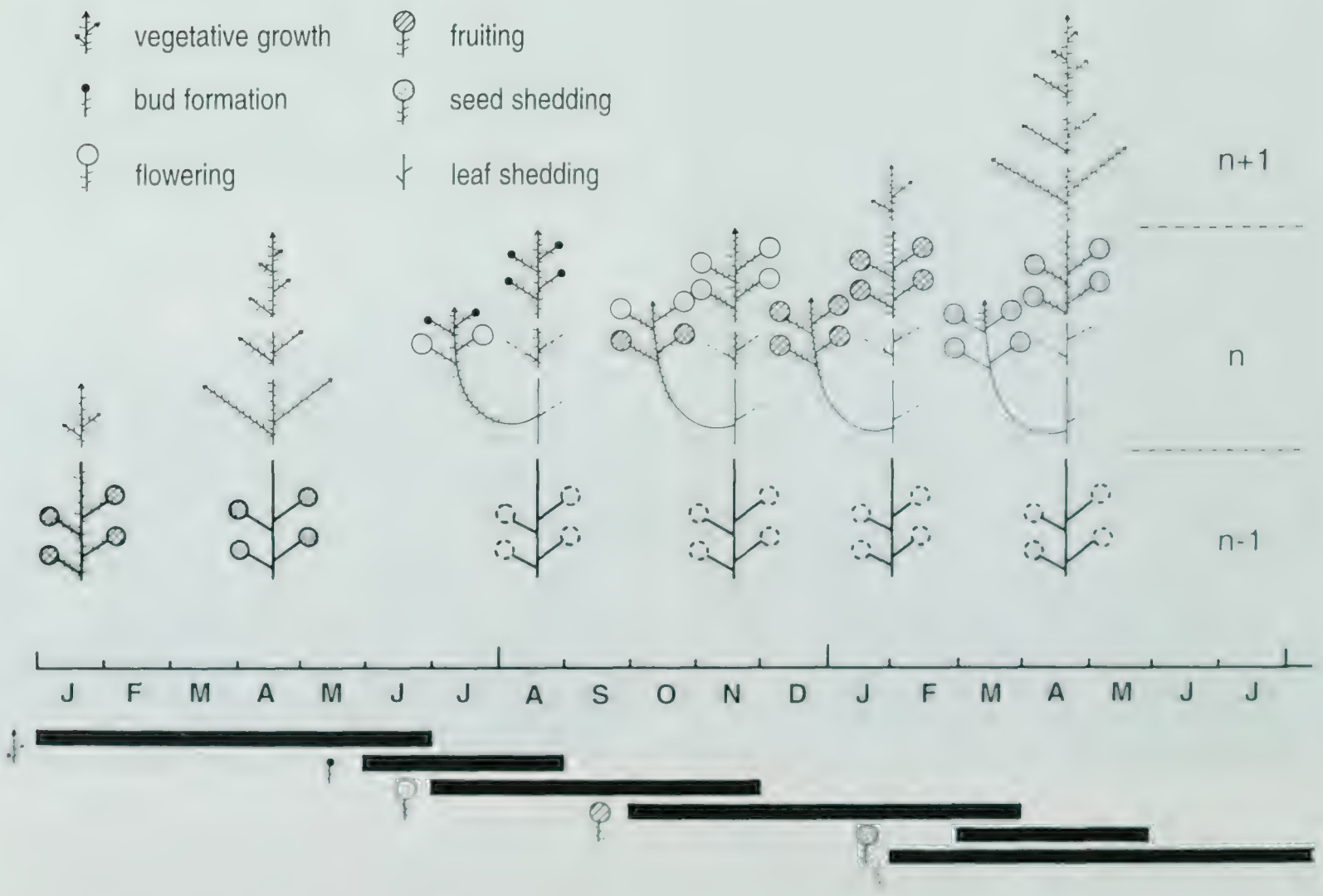


Figure 14 - **Berzelia lanuginosa.** *Phenology.* *After Le Roux et al. 1984, redrawn*

Figure 15 - **Berzelia lanuginosa**. *Aggregates of inflorescences, A, in flower, visited by many small beetles, B, after anthesis, the inflorescences turning into reddish balls with brilliant red cushions at the base of the uppermost peduncles.*

The total life span of *Berzelia* ssp. is not known, however young plants of *B. lanuginosa* (fig. 16) and *B. galpinii* (fig. 46) indicate that, in contrast to *Audouinia capitata*, the juvenile phase may be limited to a few years only. Seedlings, especially of *B. lanuginosa* (fig. 16B), are much-branched and may commence flowering in the second year. The apex remains active and continues to grow, forming monopodial units. This way orthotropous growth is promoted, resulting in a few dominant stems. With increasing age the degree of sympodial branching also increases, resulting in a more branched canopy.

The genus comprises both reseeders and resprouters. *B. lanuginosa* is a typical reseeder, with many young plants being found in nature (fig. 3C). *B. abrotanoides*, *B. burchellii*, *B. cordifolia* and *B. intermedia* have lignotubers (Carlquist 1978) and are able to resprout after a fire (fig. 21C, 36C, 38).

Berzelia ssp. resemble each other fairly closely. Individual SGUs are usually much-branched, with long (only rarely branched) sylleptic vegetative lateral shoots (svL) in the proximal region and sylleptic flowering lateral shoots (sfL) in the distal region. The leaves persist for several seasons, changing slightly in colour and surface with age and thus helping to delimit individual SGUs from each other. The latter is clearly seen in *B. incurva* and *B. commutata*, where the SGUs start with very small (fig. 34) or densely arranged (fig. 20: di) leaves. The apex usually continues to grow on for several seasons (e.g. fig. 22, 34: mc). When this dies off, lateral renewal shoots are formed above the flowering zone (e.g. fig. 20, 30, 33: R). Only a few variations have been found: occasionally renewal shoots appear within the terminal aggregate of inflorescences (e.g. *B. galpinii*, fig. 43A,B: R) or flowering lateral shoots continue the shoot system (e.g. *B. arachnoidea*, fig. 29: ia′). A single example was noted in *B. lanuginosa*, where a cataleptic flowering lateral shoot continued the shoot system, overtopping the main axis which was itself still actively growing (fig. 19: R).

All species are uniform in having only lateral inflorescences arranged in racemose (e.g. fig. 33, 34) or corymbose (e.g. fig. 18, 20, 40) clusters. Within these clusters the individual inflorescences are not densely aggregated: very often groups of about four inflorescences are separated from each other by foliated and unbranched portions of the central axis (e.g. fig. 19, 24, 37).

As regards branch order, all species have a terminal aggregate (tia) with inflorescences of 1st order and lateral aggregates (lia) with inflorescences of 2nd order. In *B. lanuginosa* (fig. 17, 18) and *B. commutata* (fig. 20) inflorescences of 3rd order of branches appear. With the exception of *B. galpinii*,

B. abrotanoides and *B. ecklonii* the inflorescences of all species show a disjunct arrangement. The flowering lateral shoots are similar to the dominant axis in having an open apex which is able to grow on in the next season and in having simple aggregates of inflorescences (e.g. fig. 24, 27) or, more rarely, indeterminate flowering lateral shoots of 2nd order (fig. 18, 19). In contrast to them the last-named three species show a conjunct arrangement of inflorescences (fig. 37, 39, 40, 43B, 48). Below the terminal aggregate of inflorescences of 1st order (I), determinate lateral shoots (dL) with a terminal (I) and additional lateral inflorescences (II) appear besides the proximal indeterminate lateral shoots (iL), indicating a transition from the simple terminal aggregate to the more complex proximal lateral shoot systems.

The flowering sequence tends to be basipetalous. As it is shown for *B. abrotanoides* (fig. 39, 40) this is not only true for the aggregates of a whole cluster but also for the inflorescences within an individual aggregate and even for the flowers of some inflorescences. The inhibition of some proximal inflorescence primordia in *B. lanuginosa*, *B. commutata* and *B.* spec. (fig. 17, 20, 27: ipi) points as well to a basipetalous decrease in reproductive capacity.

The figures illustrating the genus (13-48) are arranged after the pattern of the inflorescence clusters: starting with the most common *B. lanuginosa* and further disjunct-corymbose species (*B. commutata*, *B. intermedia*, *B. burchellii*), the disjunct-racemose species (*B.* spec., *B. arachnoidea*, *B. incurva*) are presented. Finally the species with conjunct inflorescence clusters are illustrated (*B. galpinii*, *B. abrotanoides*, *B. ecklonii*).

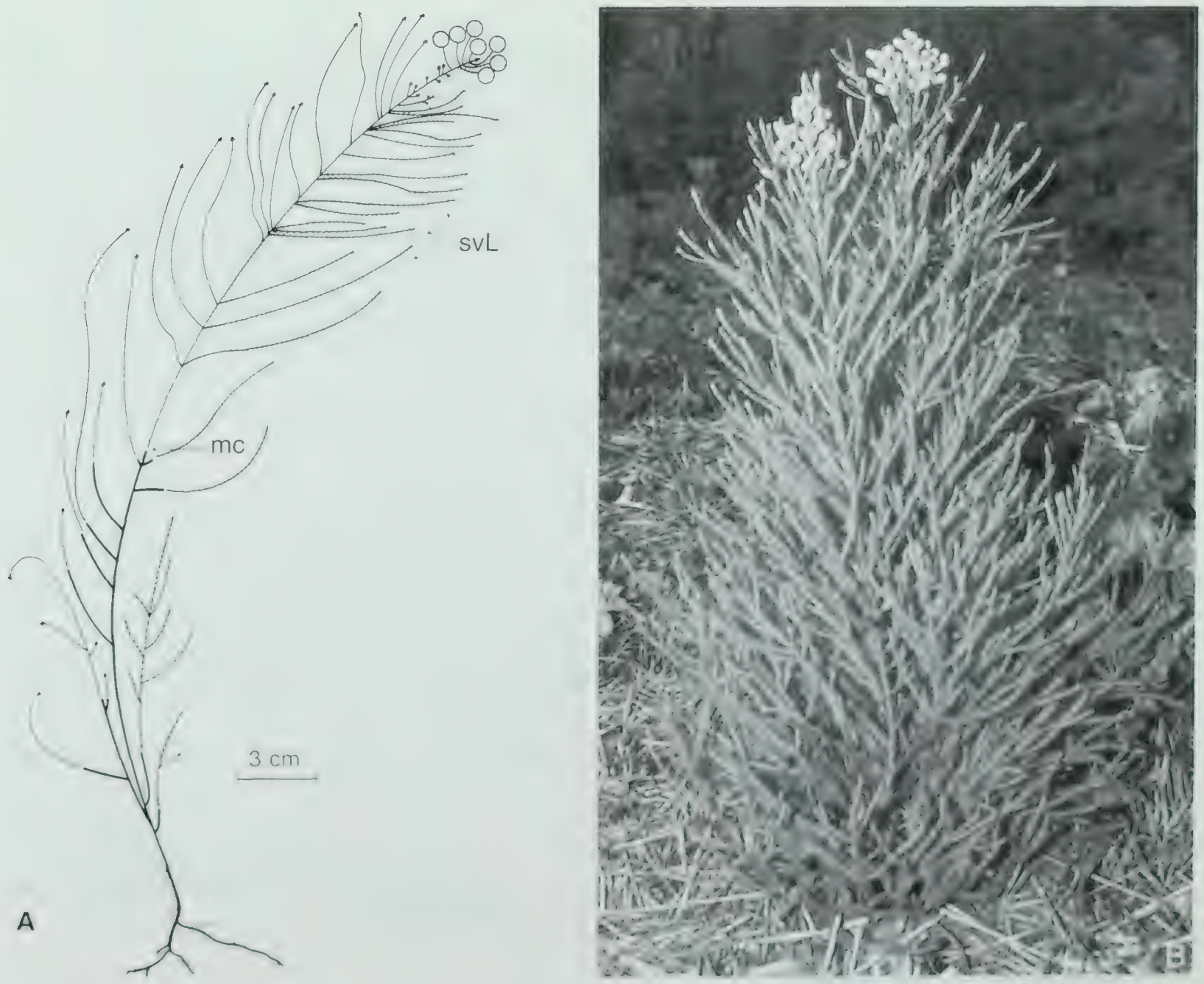


Figure 16 - **Berzelia lanuginosa**. *Young plants with a characteristically rich sylleptic branching: A, profile of a two season old seedling found in nature, B, habit of a seedling cultivated at Kirstenbosch Botanic Garden*

Figure 17 - **Berzelia lanuginosa.** *Profile of a flowering shoot system, three seasons old, with the characteristic high degree of vegetative branching (grey) and the corymbose pattern of inflorescences* (I-III). *The proximal inflorescence primordia often are inhibited indicating a decrease of the reproductive capacity (*ipi).

Figure 18 - **Berzelia lanuginosa.** *Profile of a flowering seasonal growth unit (*SGU*), with only the vegetative part outlined. Besides the terminal aggregate of inflorescences (*tia*) lateral aggregates of the 1st and 2nd order are present (*lia*). Sylleptical vegetative lateral shoots (*svL*) appear between the individual aggregates.*

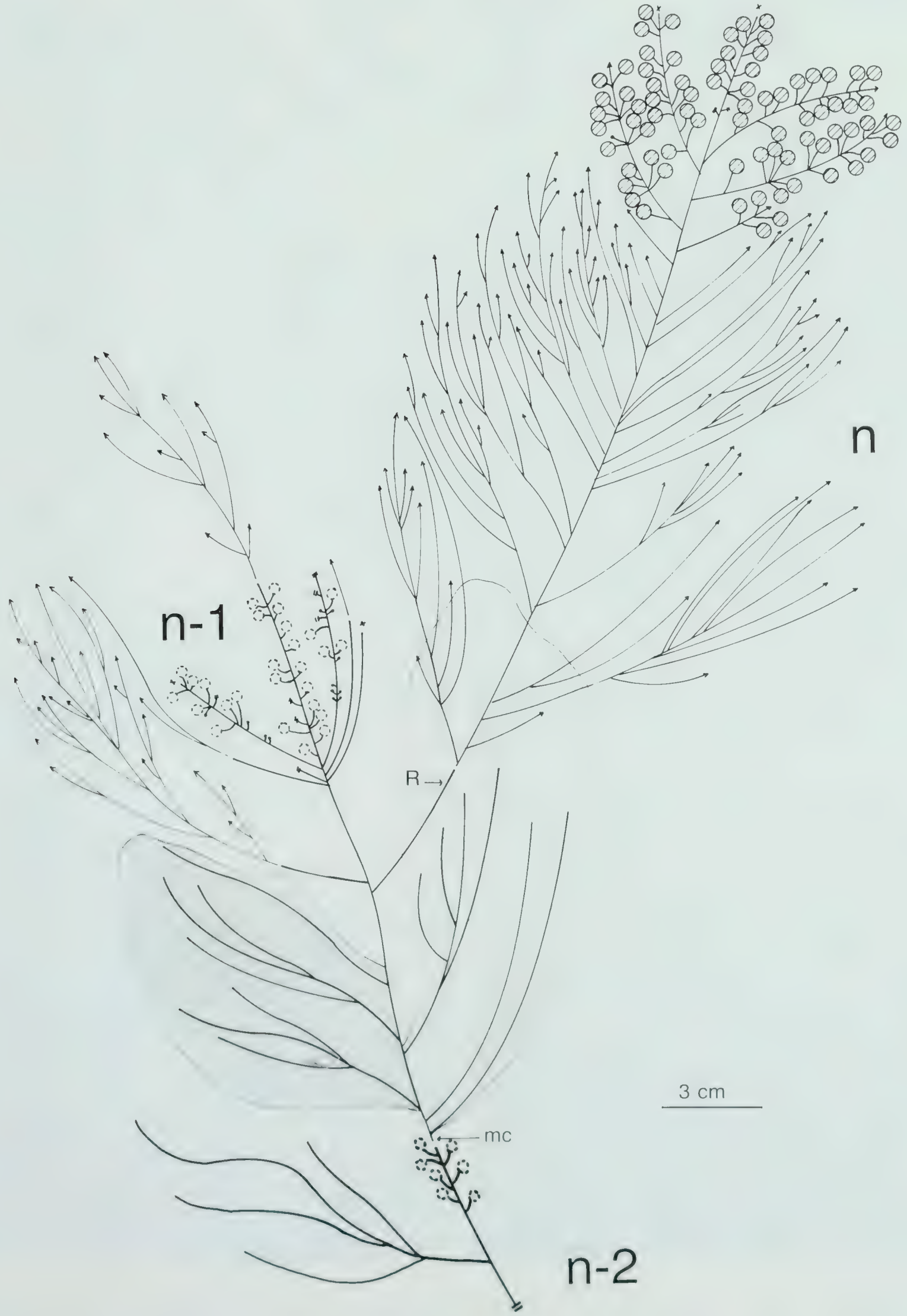


Figure 19 - **Berzelia lanuginosa**. *Profile of a flowering shoot system showing the overtopping of the former main axis by a cataleptic flowering lateral shoot (R).*

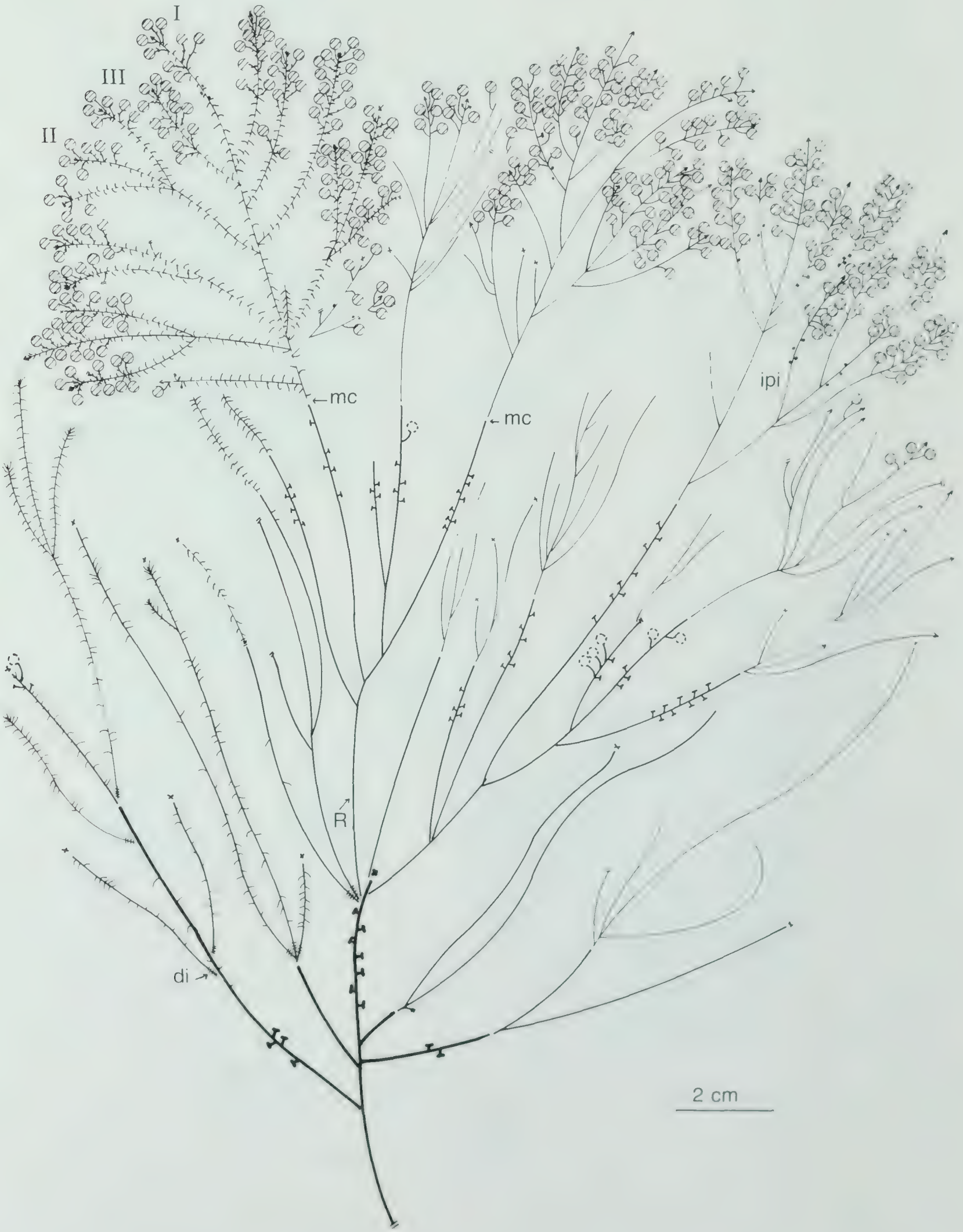


Figure 20 - **Berzelia commutata**. *Profile of a flowering shoot system, three seasons old, with lateral inflorescences of the 1st , 2nd and 3rd order of branches* (I-III). *Note that nearly all lateral shoots come to flower syllepticaly and that the primordia of the proximal inflorescences are occasionally inhibited* (ipi).

di, *dense internodes.*

Figure 21 - **Berzelia intermedia**. *A, flowering plant, about 3 m high, at a locality in the Langeberg area, Grootvadersbos Nature Reserve, B, flowering shoot system, two seasons old, with conspicuous pincushion-like inflorescences C, renewal from the base after a fire, D, pollen-feeding beetles are often found crawling among the exserted stamens.*

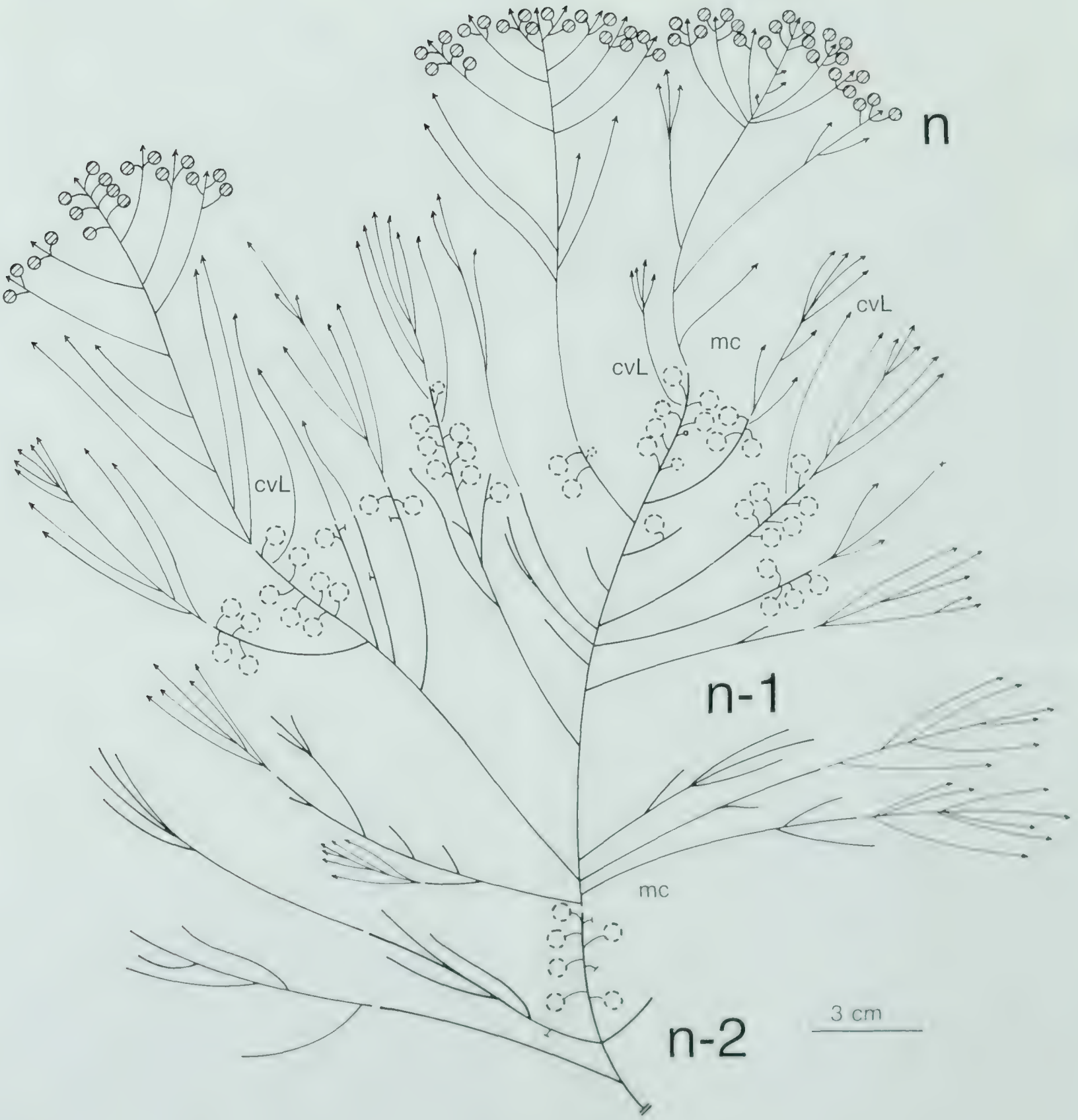


Figure 22 - **Berzelia intermedia**. *Profile of a flowering shoot system, three seasons old. Note the high degree of monopodial connections (*mc*) even at the lateral shoots, the basitonous influence in the inflorescence cluster resulting in a corymbose pattern, the appearance of sylleptic vegetative lateral shoots between the individual aggregates and the cataleptic vegetative lateral shoots (*cvL*) below the uppermost inflorescences.*

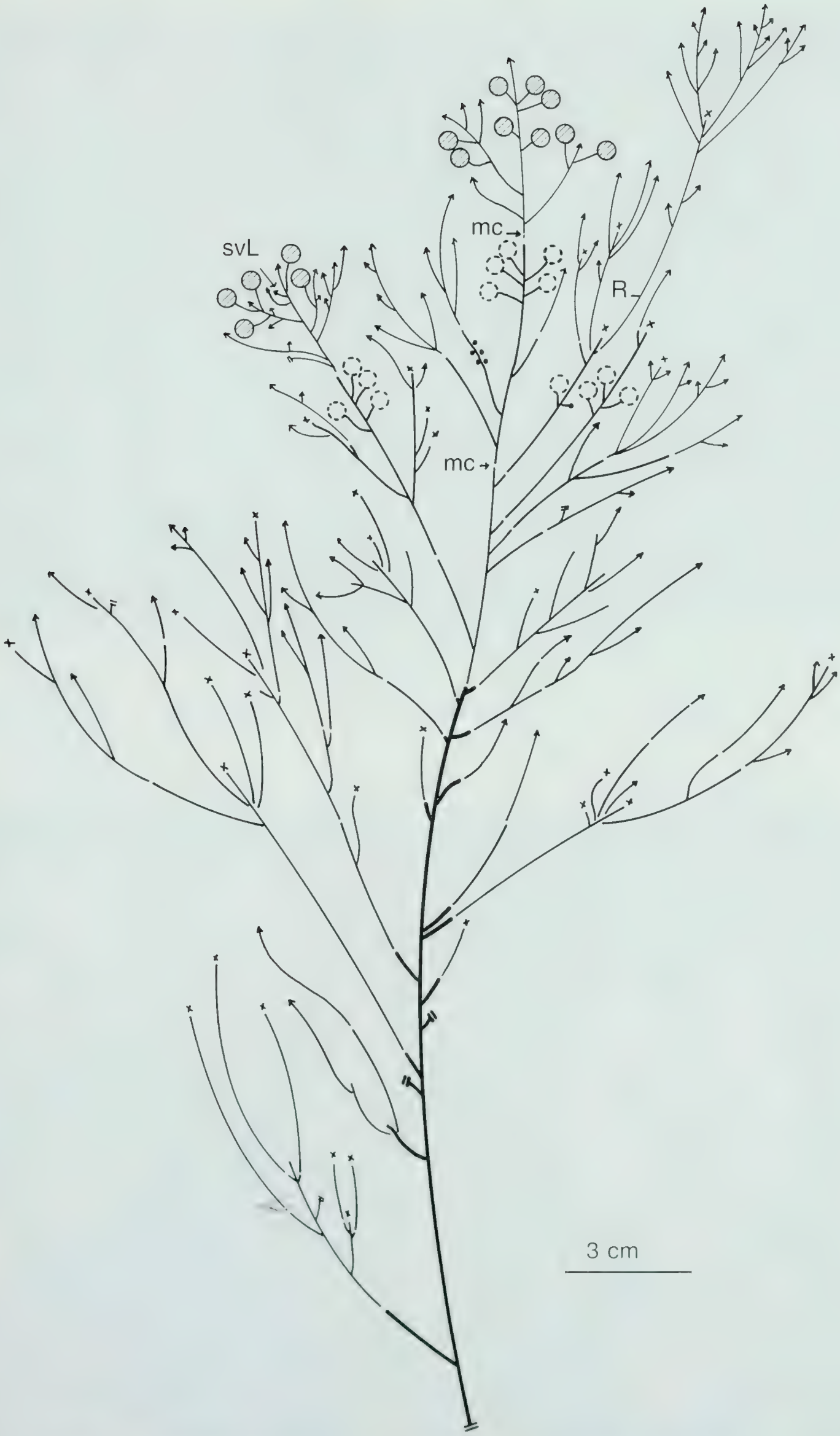


Figure 23 - **Berzelia intermedia**. *Profile of a flowering shoot system, four seasons old. Compared with the profile in fig. 22 the shoot system seems to be exhausted: the SGUs become remarkably smaller, the inflorescence clusters only have a few inflorescences and the lateral branches tend to die off after one season, showing a sympodial pattern, while the dominant shoot is still growing on.*

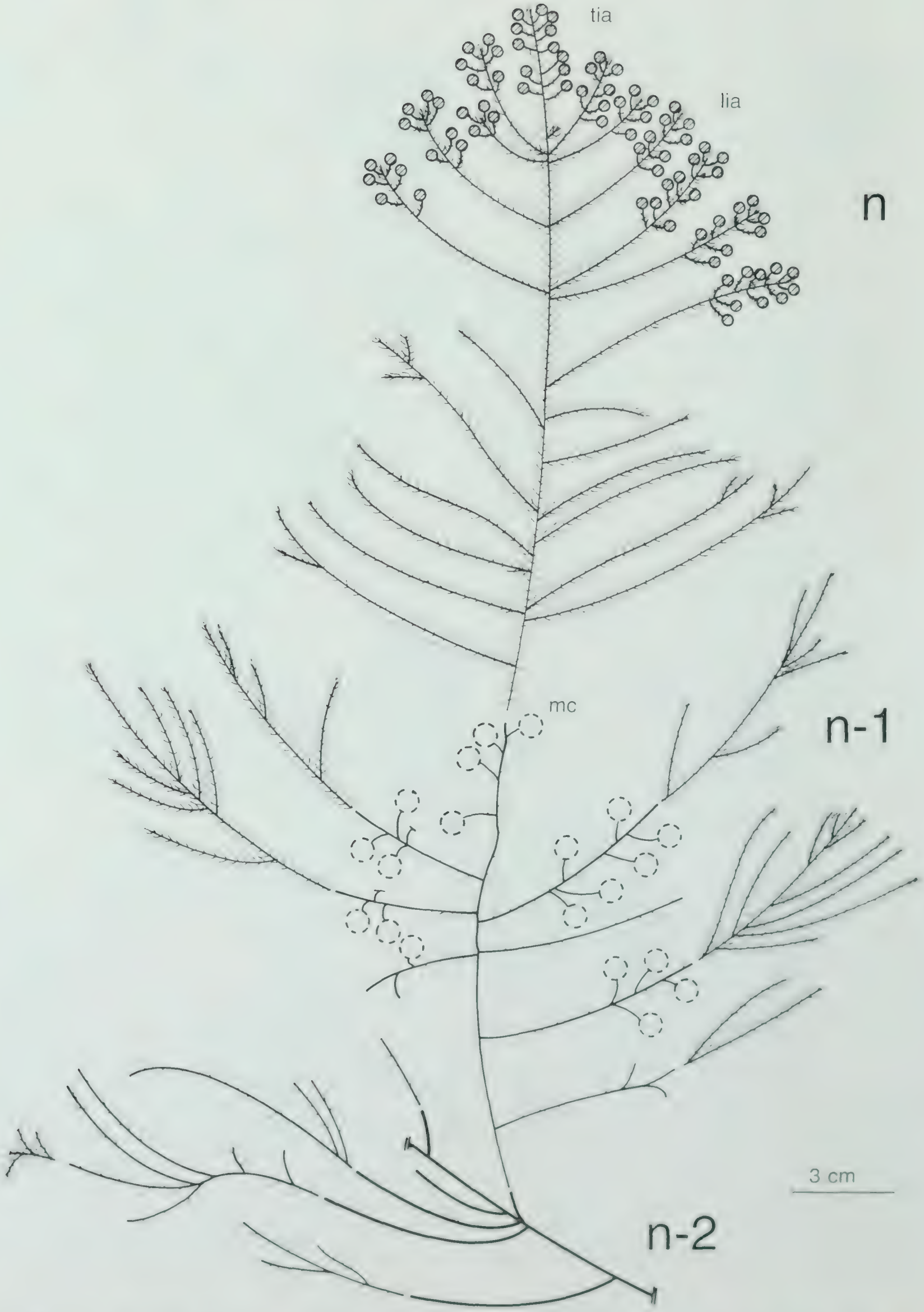


Figure 24 - **Berzelia burchellii.** *Profile of a flowering shoot system, three seasons old. The cluster of inflorescences is disjunct, but because of the basitonous influence it looks like a corymb. Note the high degree of monopodial connections and the clear difference in foliage between the SGUs*

Figure 25 - **Berzelia burchellii**. *A, a plant about 50 cm high at a locality in the Langeberg area (Rooiwaterspruit, Grootvadersbos Nature Reserve), B, cluster of inflorescences in the prefloral phase.*

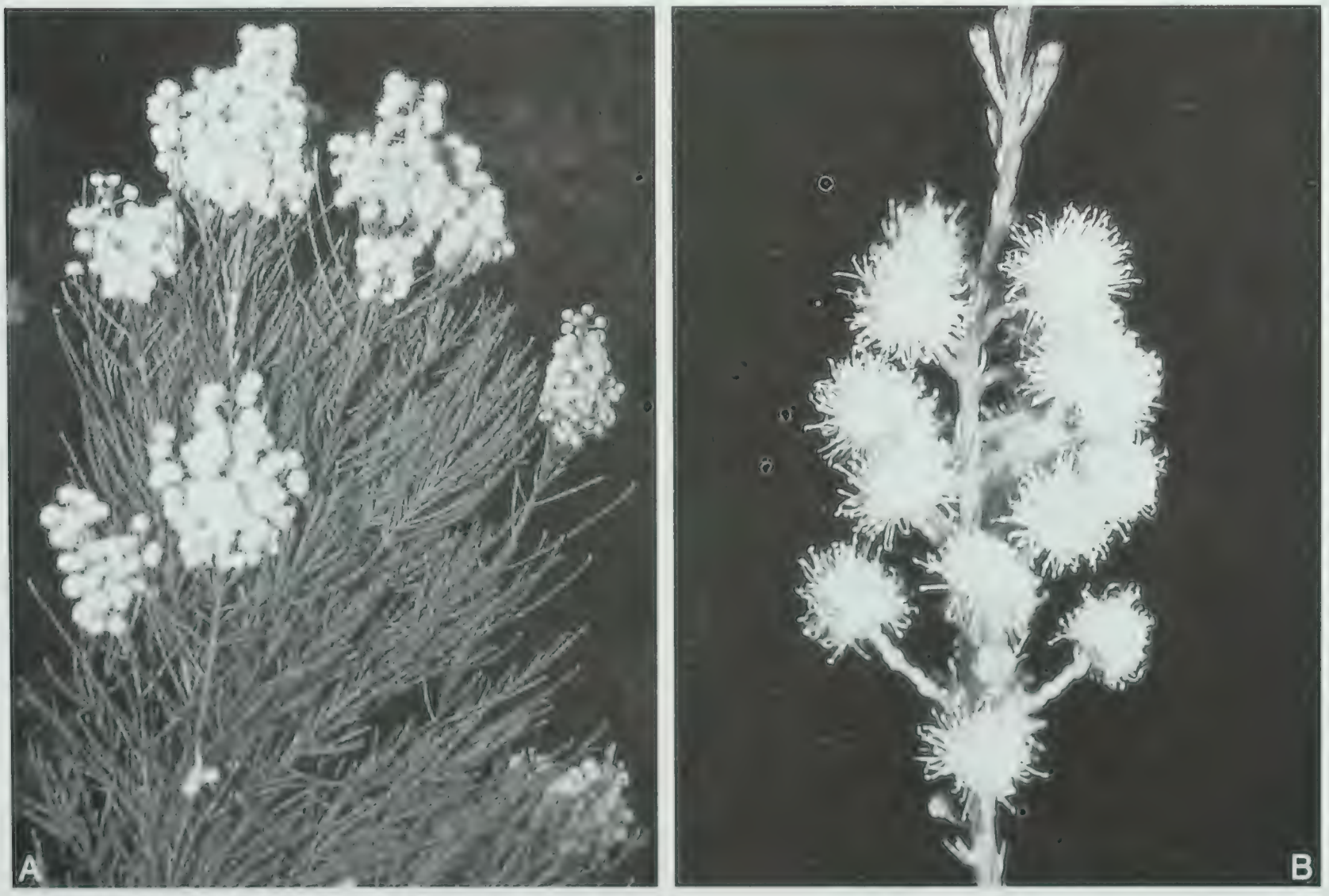


Figure 26 - **Berzelia** *spec. A, flowering plant cultivated at Kirstenbosch Botanic Garden, B, cluster of loosely aggregated, pincushion-like inflorescences*

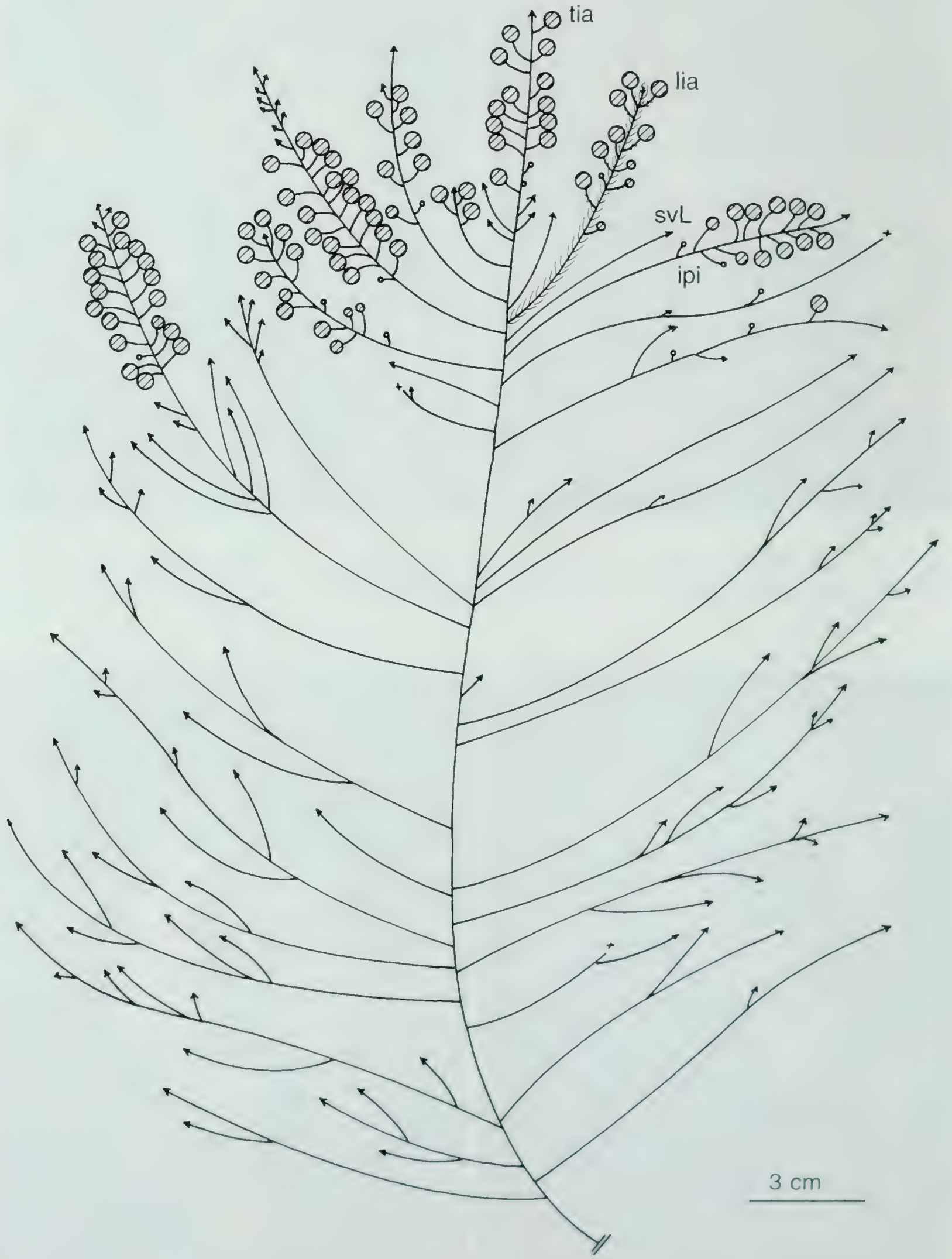


Figure 27 - **Berzelia *spec***. *Profile of a SGU with a terminal (*tia*) and several lateral inflorescence aggregates (*lia*) and sylleptic vegetative lateral shoots (*svL*) in between. Note the high grade of branching in the proximal part of the SGU and the inhibition of some inflorescences.*

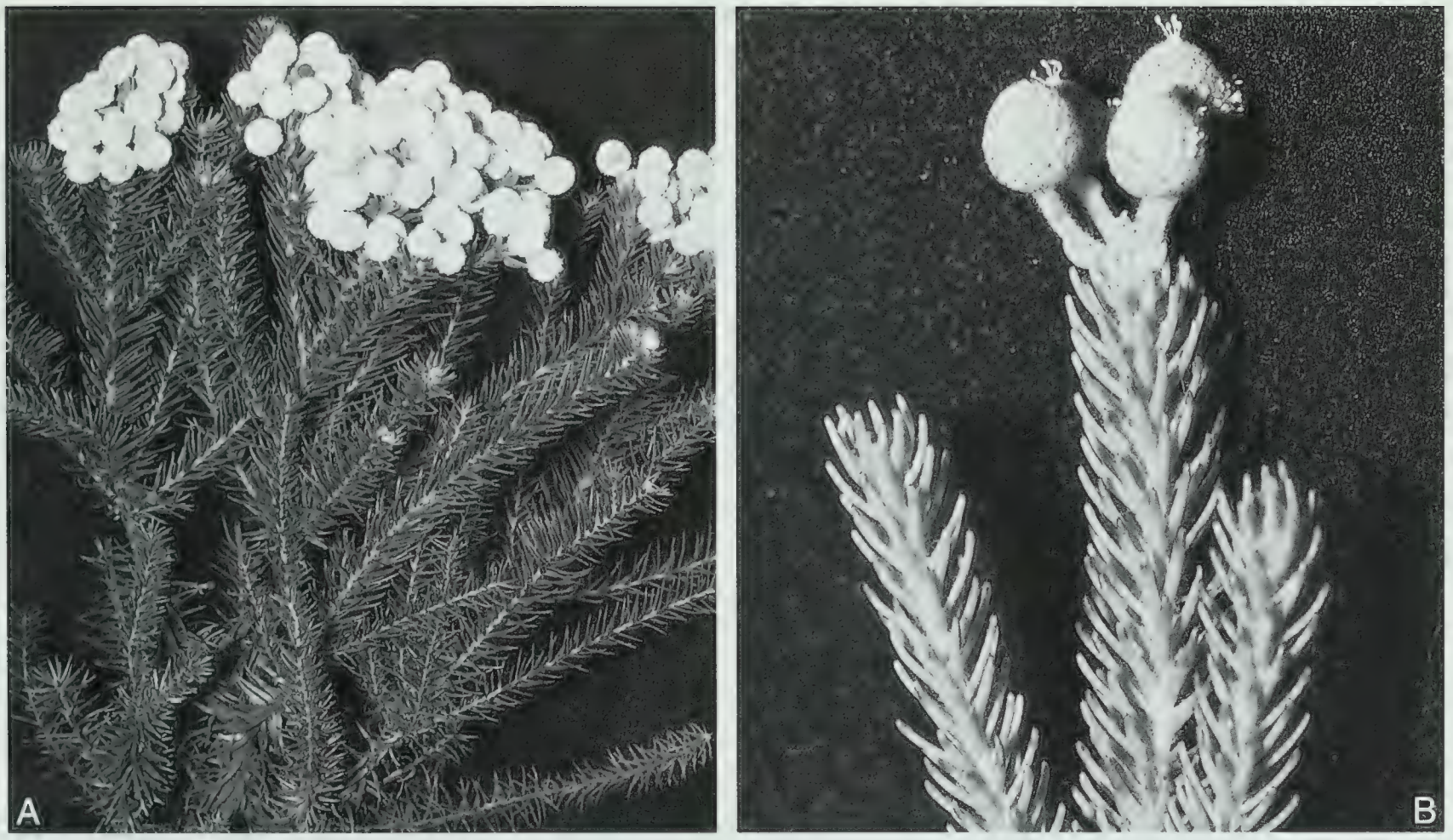


Figure 28 - **Berzelia arachnoidea**. *A, flowering plant about 70 cm high at a locality in the Hottentots Holland Mountains (Nuweberg Forest Reserve), B, part of a very weak plant cultivated at Kirstenbosch Botanic Garden; in each of the few inflorescences the terminal flower opens at first.*

Figure 29 - **Berzelia arachnoidea**. *Profile of a flowering shoot system with three SGUs. The inflorescences are arranged in a disjunct-racemose pattern, sylleptic vegetative lateral shoots (*svL*) appear among the individual aggregates. Usually the shoot system is renewed above the terminal inflorescence aggregate (*tia*), but in one case a lateral shoot overtops the main axis (*lia*)*

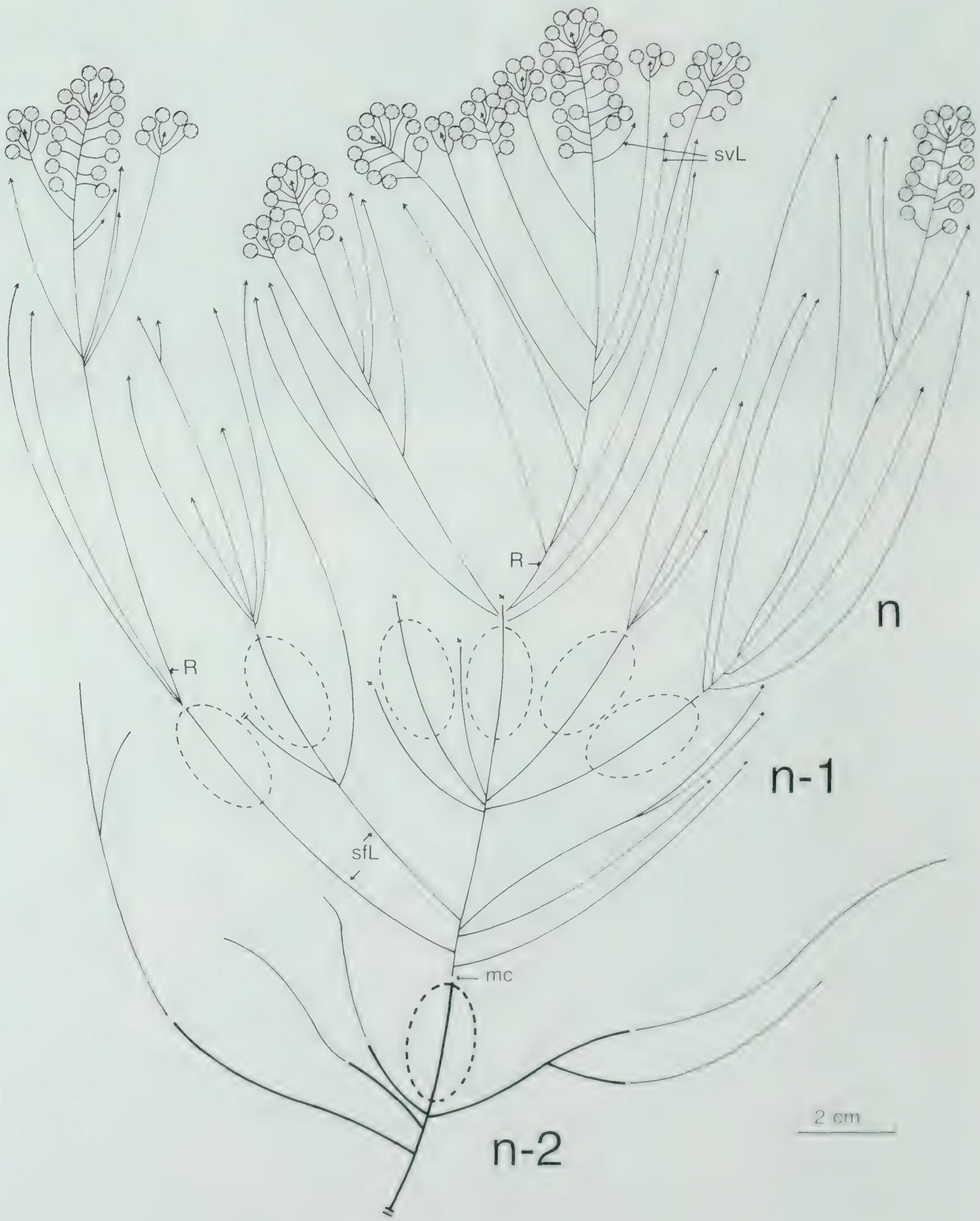


Figure 30 - **Berzelia arachnoidea**. *Profile of a flowering shoot system, three seasons old, showing monopodial and sympodial connections of SGU's.*

Figure 31 - **Berzelia rubra**. *A,B, habit of two plants from the Hottentots Holland Mountains, each being in the postfloral phase: A, at Landrostkop, about 80 cm high, B, at Nuweberg Forest Reserve, about 1,5 m high with a small stem and a heavy canopy. C, disjunct cluster of inflorescences having turned into reddish 'balls' in the postfloral phase. D, cluster of inflorescences: below: deflorated, above: flowering inflorescences interspersed with renewal shoots (compare with fig. 32)*

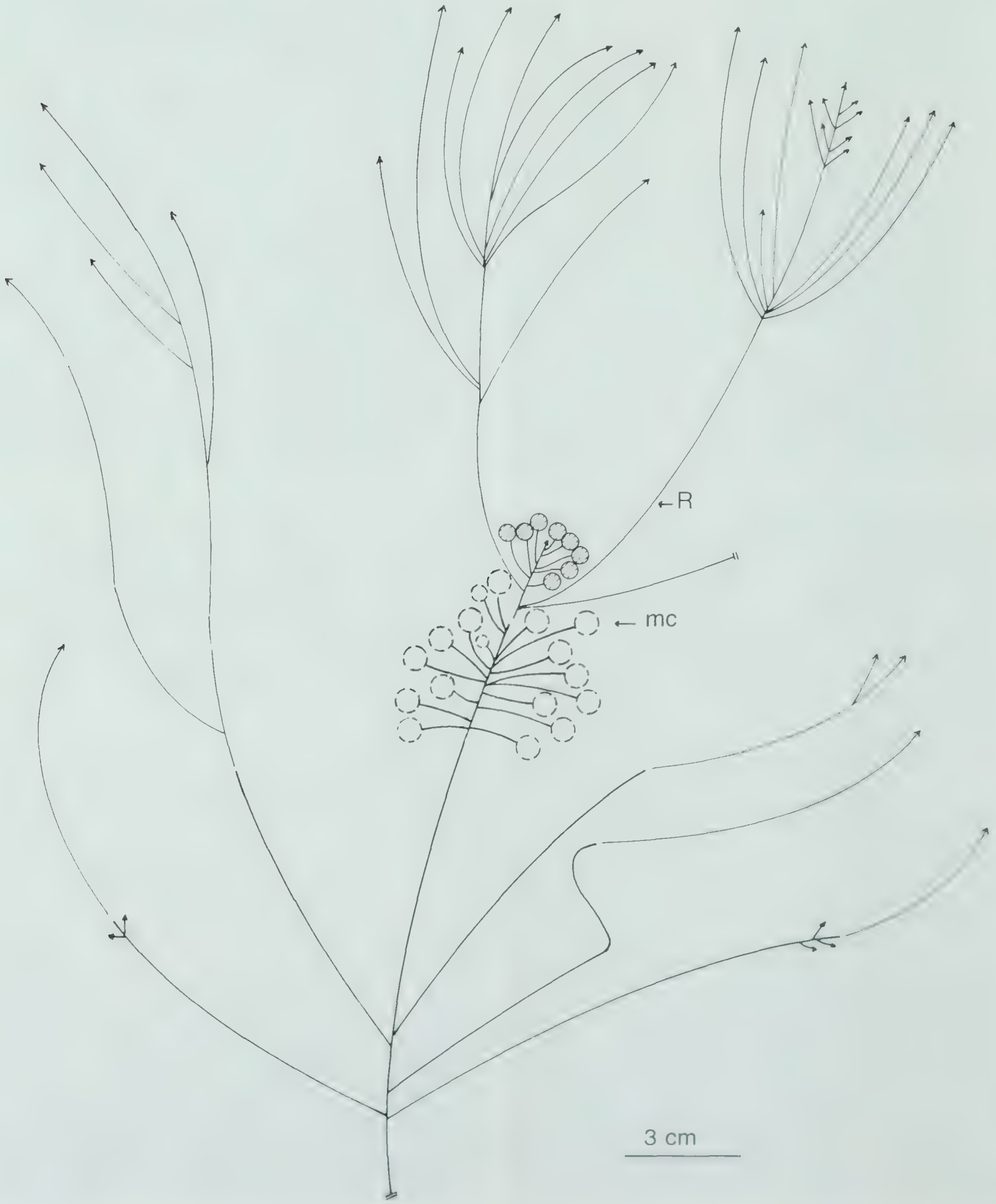


Figure 32 - **Berzelia rubra**. *Profile of the flowering shoot system shown in fig. 31D. The interpretation is not clear: if it is only one SGU the flowering sequence and the position of the renewal shoots are irregular, if there are two SGU's (as suggested here) the main axis is irregularly inhibited.*

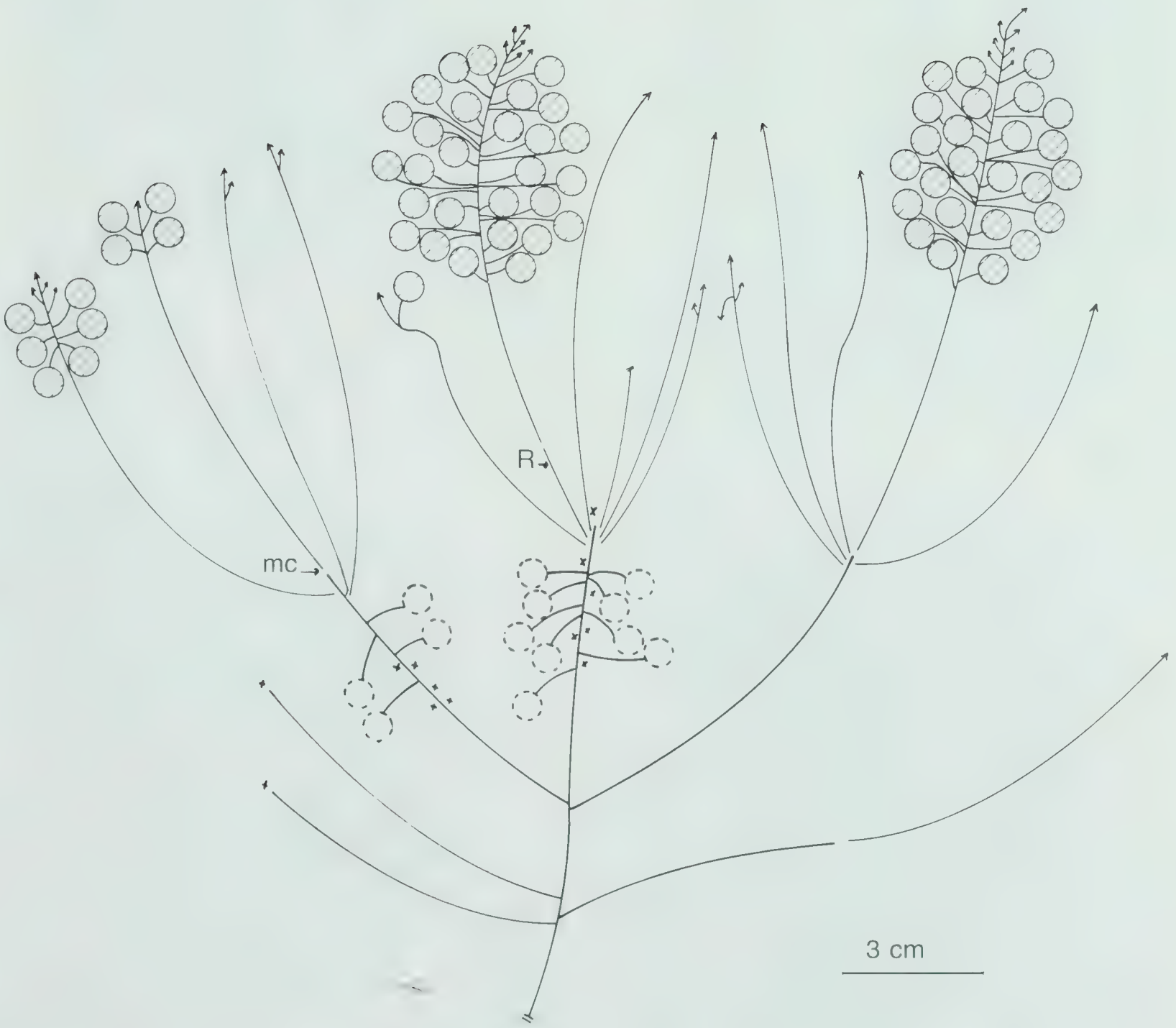


Figure 33 - **Berzelia rubra**. *Profile of a flowering plant, two seasons old. Note, in the case of sympodial connection, the distal position of the renewal shoots (R); occasionally only the terminal aggregate of inflorescences is present.*

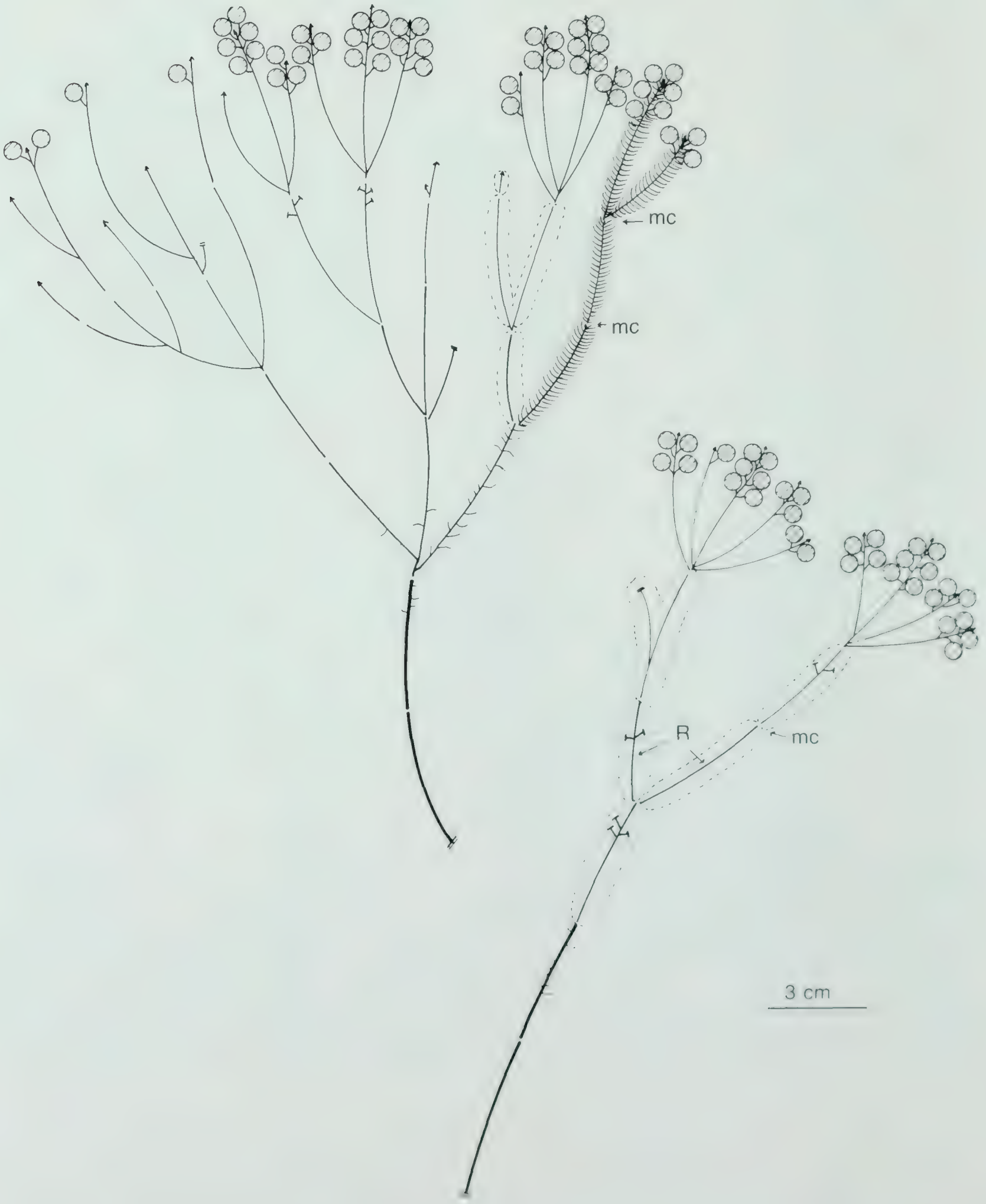


*Figure 34 - **Berzelia incurva**. Profiles of flowering shoots systems. Note the first small leaves in each SGU, the sparse branching and the small clusters of inflorescences.*

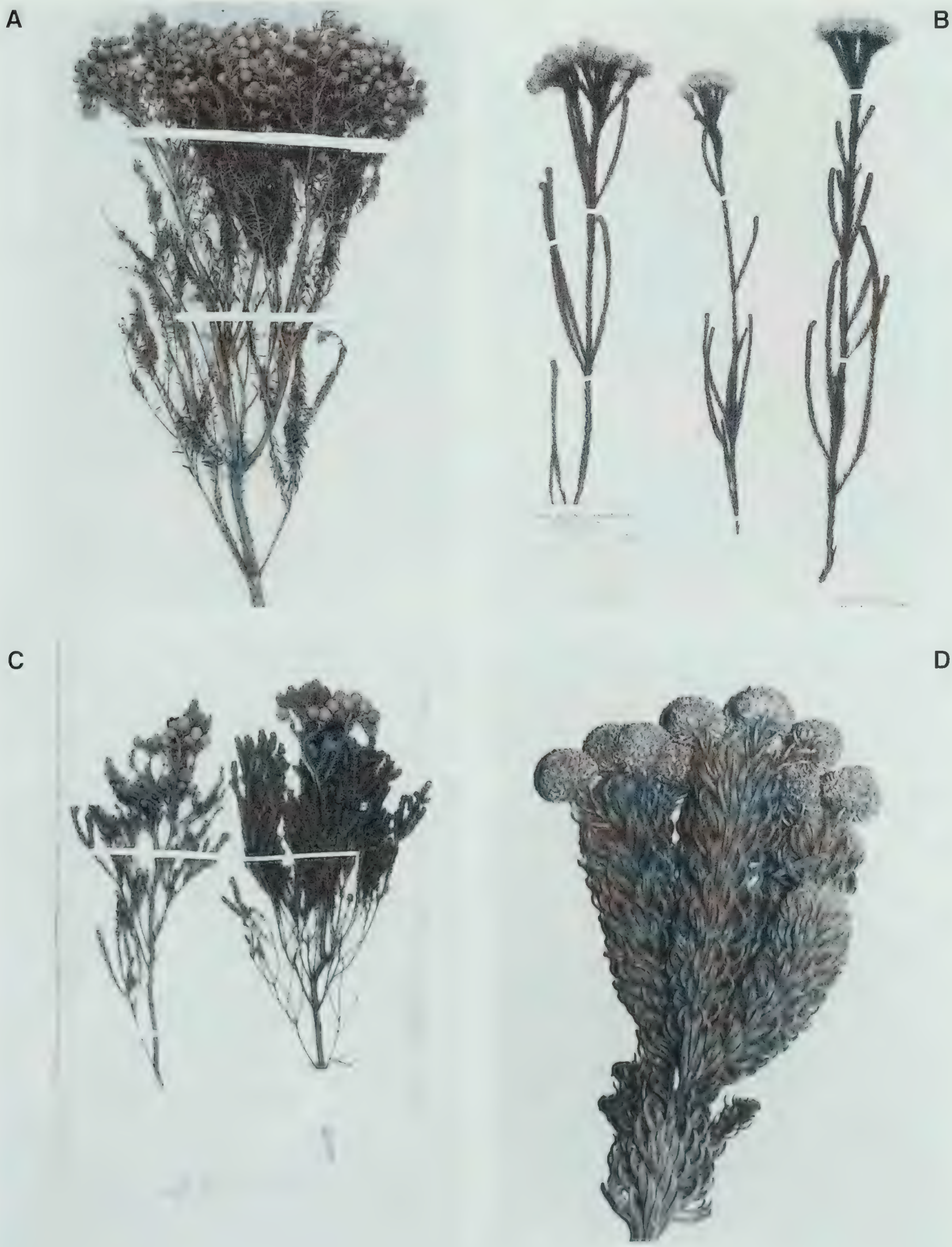


Figure 35 - **Berzelia.** *A*, B. commutata *(Herb. Engler s.n., B)*, *B*, B. ecklonii *(Rourke 983, B)*, *C*, B. intermedia *(H.G. s.n., B)*, *D*, B. incurva (Williams 2269, NBG).

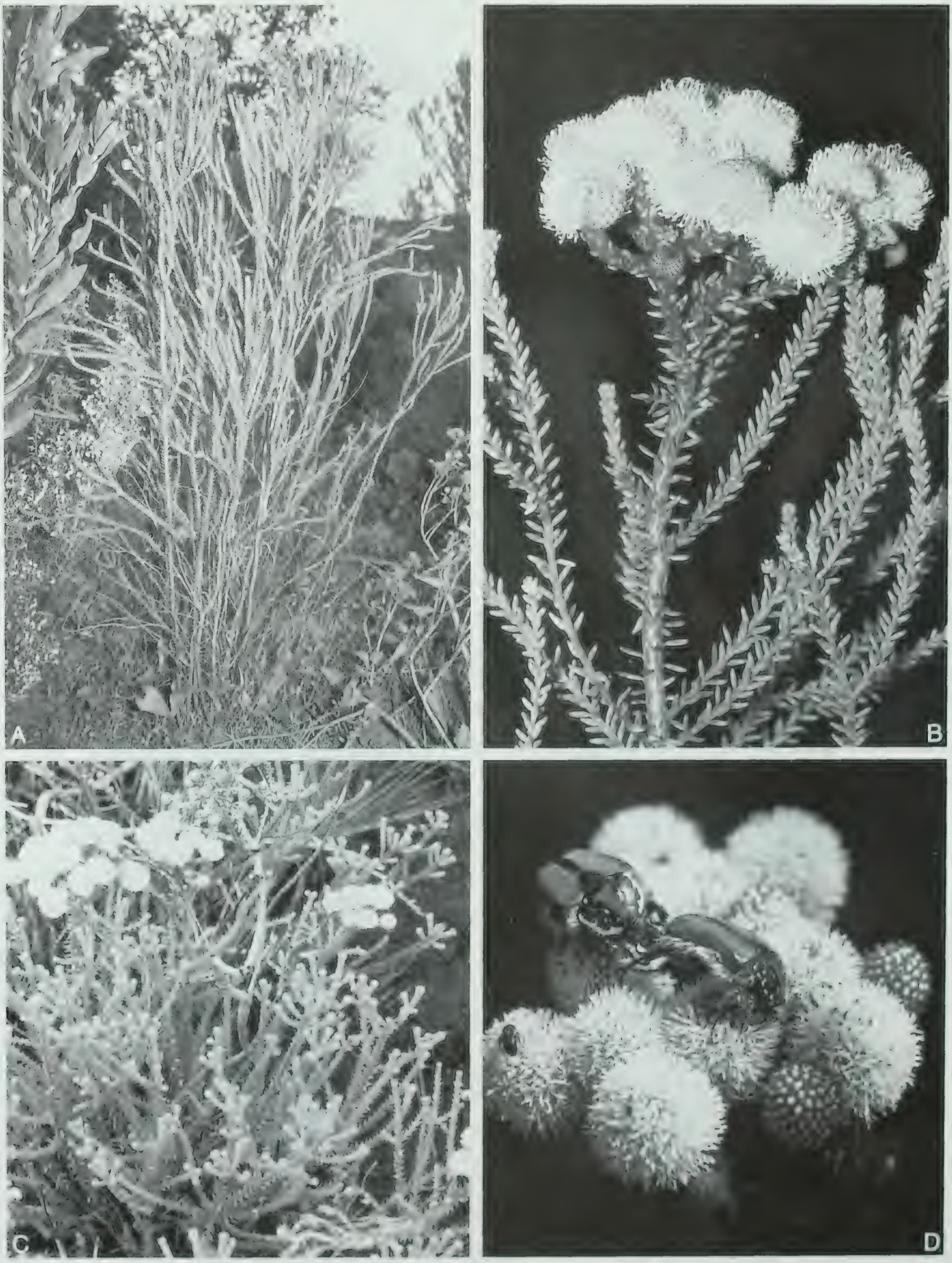


Figure 36 - **Berzelia abrotanoides** *A, an erect slender plant cultivated at Kirstenbosch Botanic Garden about 1,5 m high, B, flowering shoot system, C, a low plant, about 40 cm high, resprouted after a fire, at a locality in the Cape Point Nature Reserve (compare with fig. 38) D, inflorescences in full flower, visited by pollen-feeding beetles*

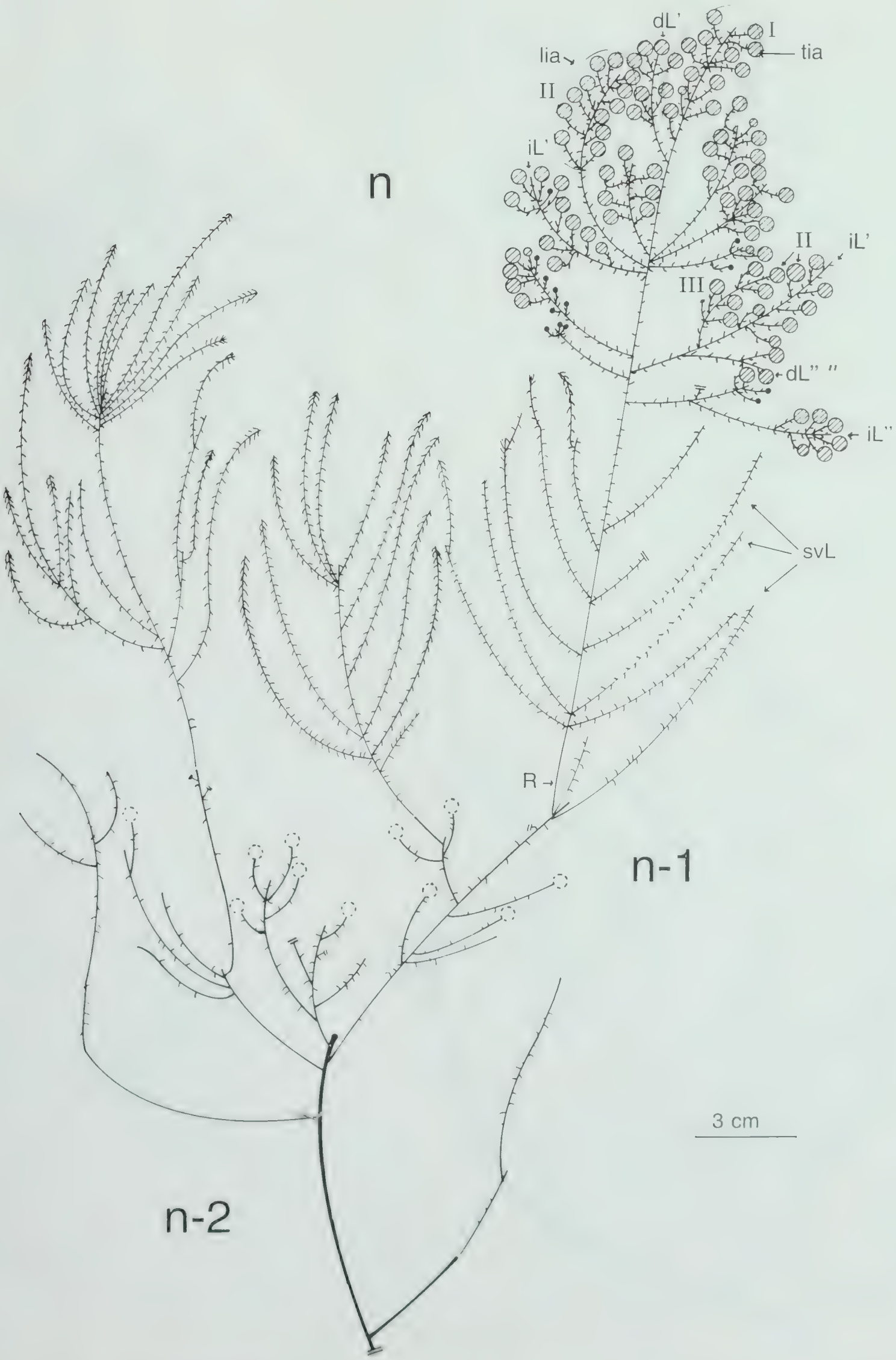


Figure 37 - **Berzelia abrotanoides**. *Profile of a flowering shoot system, three seasons old. The cluster of inflorescences is conjunct with determinate and indeterminate lateral shoots (*dL, iL*). Nearly all of the numerous sylleptic vegetative shoots (*svL*) remain unbranched.*

Figure 38 - **Berzelia abrotanoides**. *Profile of a resprout from the base after a fire (compare with fig. 36C)*

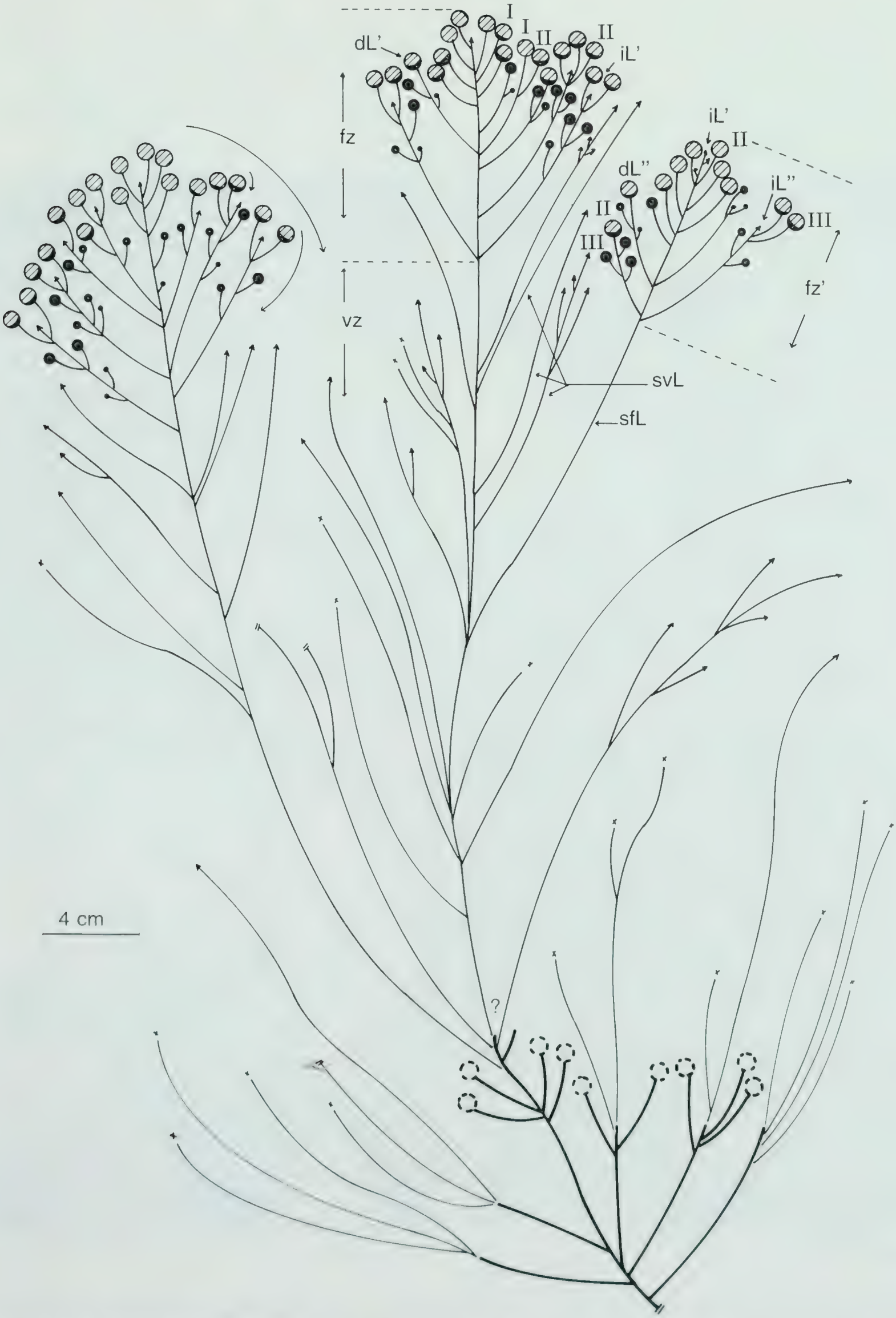


Figure 39 - **Berzelia abrotanoides**. *Profile of a flowering shoot system, two seasons old. Note the medial position of the sylleptic flowering lateral shoot (sfL), the conjunct cluster of inflorescences and the basitonous flowering sequence (arrows)*

Figure 40 - **Berzelia abrotanoides**. *Profile of a flowering shoot system, three seasons old. Note the basitonous flowering sequence (arrow), the corymbose habit and the conjunct nature of the inflorescence cluster*

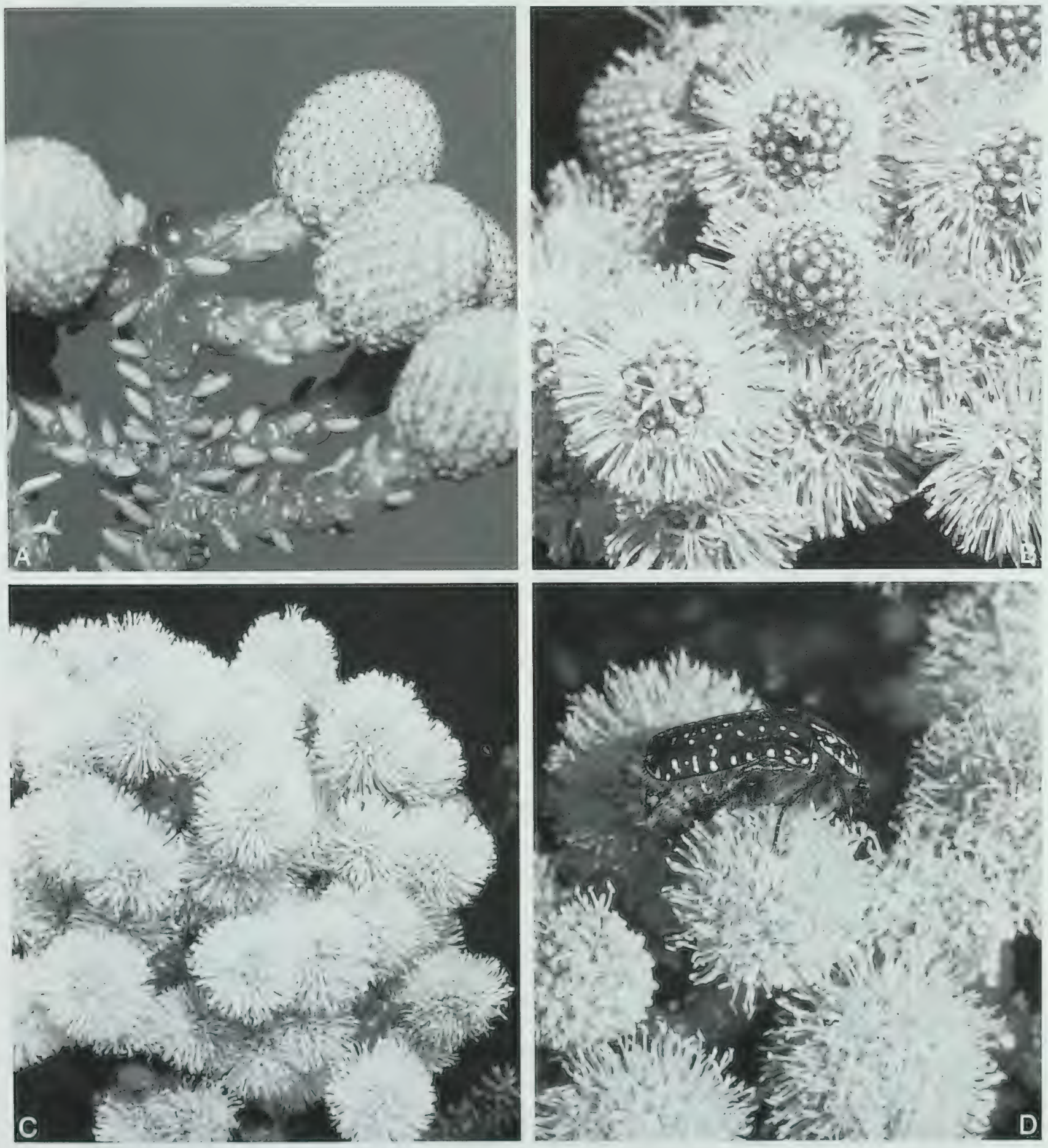


Figure 41 - **Berzelia abrotanoides**. *Clusters of inflorescences: A, in the prefloral phase showing the brilliant red cushions at the base of the peduncles, B, at early anthesis showing the flowering sequence which starts at the terminal flower and then continuous from the middle in a divergent way, C,D, in full flower showing the pincushion-like habit. The inflorescences are often visited by pollen-feeding beetles (D)*

Figure 42 - **Berzelia galpinii**. *A, flowering shrub of about 1 m height at a fynbos locality in the Langeberg area, Grootvadersbos Nature Reserve, B, C, flowering plants of about 1,5 m height at Kirstenbosch Botanic Garden showing the characteristic growth form of many* Berzelia *ssp. with one or a few thin stems and a heavy, richly branched flowering canopy, D, flowering shoot system showing the large deflorated inflorescences of the last season, the main axis growing on and at the top the cluster of recent inflorescences in bud*

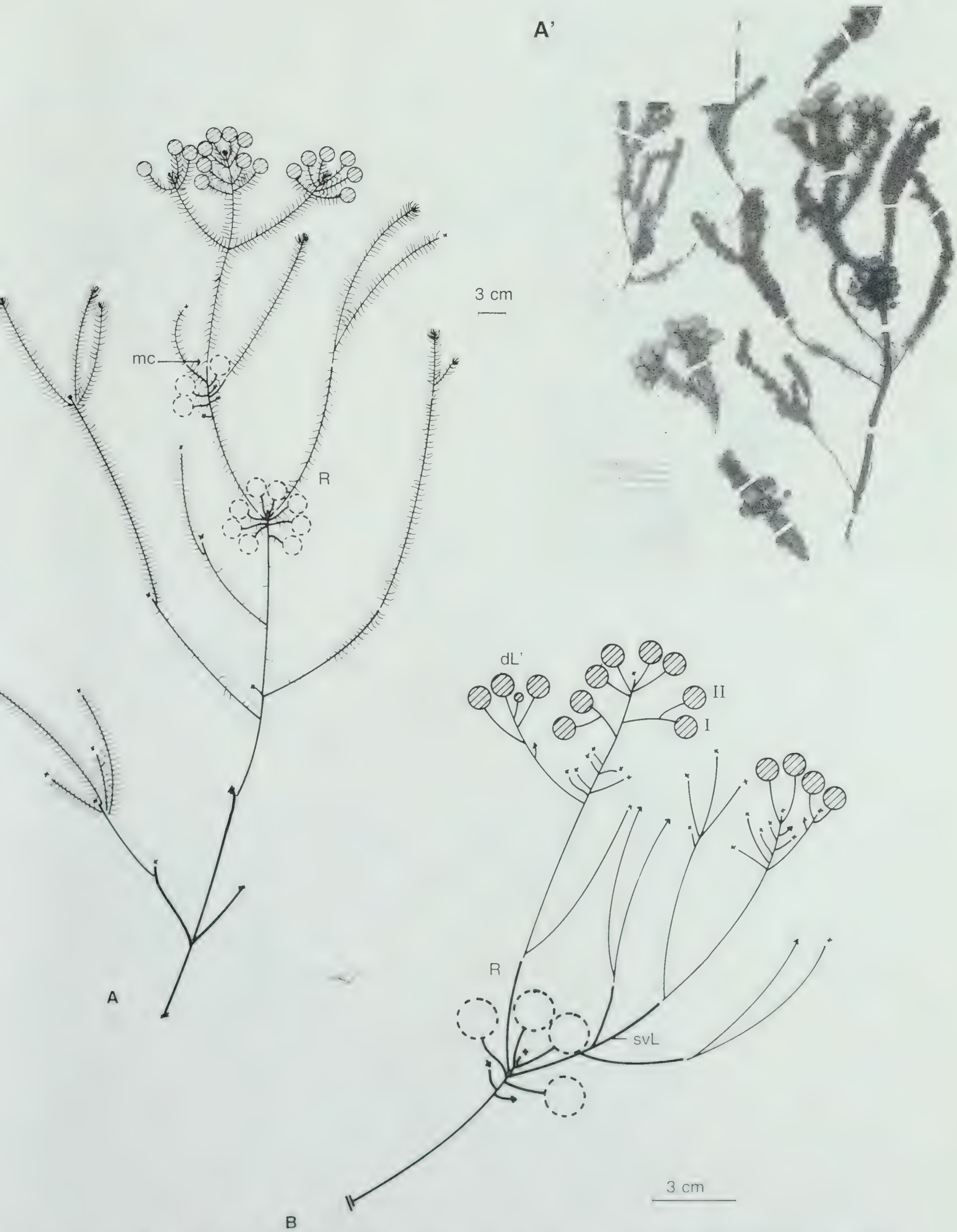


Figure 43 - **Berzelia galpinii**. *A, B, profiles of flowering shoot systems, both showing renewal shoots (R) arising within the inflorescence clusters, A' herbarium specimen (Powrie 153,B), from which fig. 43A has been copied.*

Figure 44 - **Berzelia galpinii**. *Profile of a four season old shoot system at the end of anthesis, already starting to sprout again. Note the monopodial and sympodial connections between subsequent SGUs and the appearance of sylleptic vegetative lateral shoots* (svL) *among the inflorescences*

Figure 45 - **Berzelia galpinii**. *Profile of a flowering shoot system with a renewal shoot (R) arising from the growing apex of a flowering lateral shoot.*

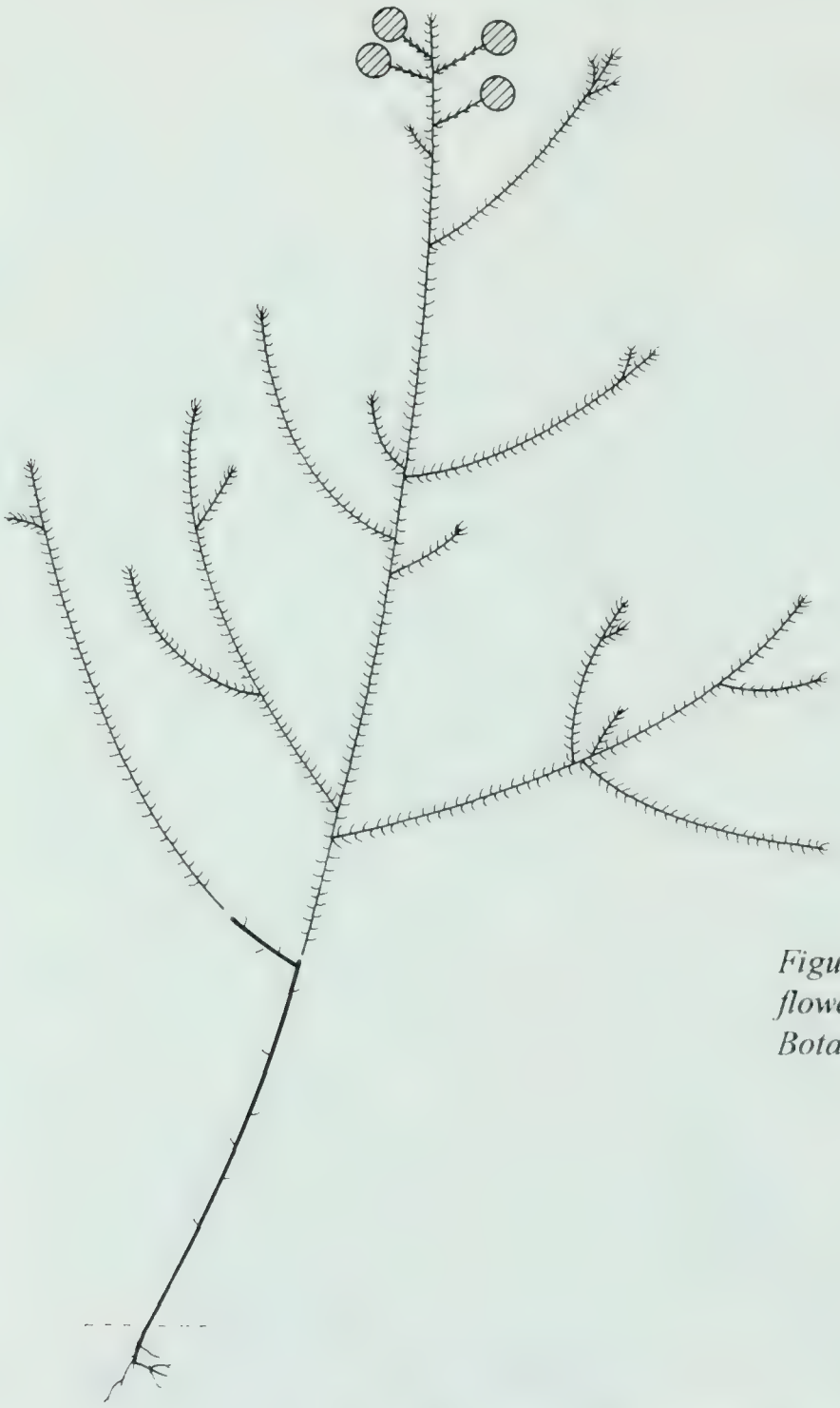


Figure 46 - **Berzelia galpinii**. *Young plant, already flowering in the second season (seen at Kirstenbosch Botanic Garden).*

Figure 47 - **Berzelia galpinii.** *The pincushion-like inflorescences are in full flower and visited by many pollen-feeding beetles*

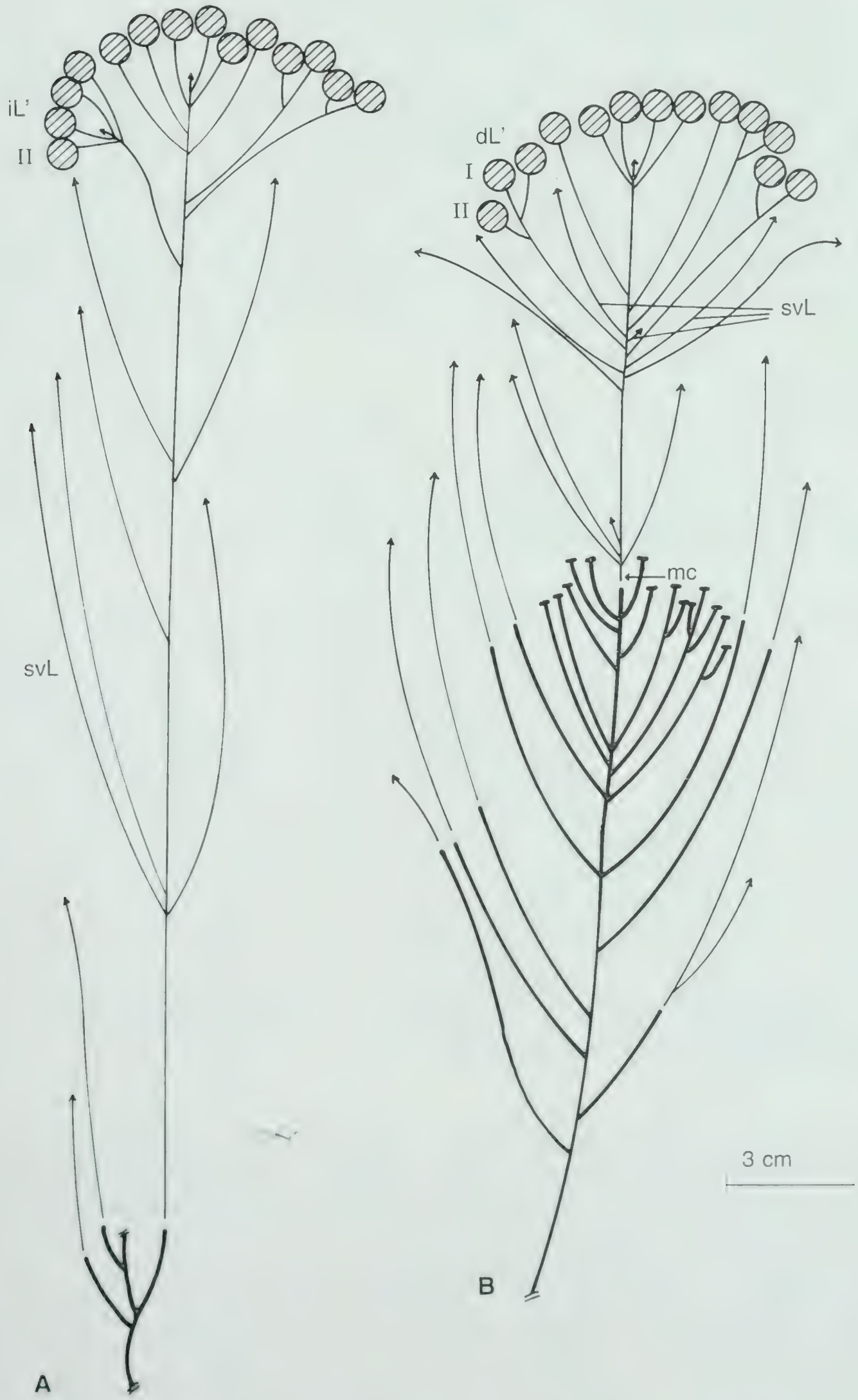


Figure 48 - **Berzelia ecklonii**. *Profile of flowering shoot systems. Note the conjunct nature of the corymb-like cluster of inflorescences and the unbranched vegetative shoots*

Leaf metamorphosis and inflorescence structure. The inflorescences of all species are very similar to each other. They resemble pincushions, have a white to yellowish colour and are not larger than one centimeter in diameter. About 100 florets (50-300; fig. 49C) are densely aggregated and individuals are indistinguishable when in full flower owing to the presence of long, exserted stamens (e.g. fig. 15A, 21B,D, 26B, 36B,D, 41, 47).

The remarkable flowering sequence points to the structure of the individual inflorescences. Though occasionally irregular, a divergent flowering sequence is very often present. Together with the first axillary flowers, a flower at the top of the 'head' opens (fig. 41B) which is interpreted as the terminal flower of the inflorescence. Such a terminal flower has been found in *B. abrotanoides* (fig. 41B), *B. commutata*, *B. burchellii* and *B. arachnoidea* (fig. 28B) and may also be present in *B. incurva* (Burman & Bean, 1985: 103). Occasionally some sterile bracts surround the terminal flower. Although a similar phenomenon could not be demonstrated in the remaining species, nothing contradicts the supposition that all species of the genus *Berzelia* have determinate inflorescences. Each flower being subtended by a bract and by two bracteose prophylls, the inflorescences are therefore interpreted as cephaloids (fig. 49A) that is reduced determinate inflorescences, and not as simple heads as the initial impression suggests.

The inflorescences are always arranged laterally on determinate bracteate short-shoots (fig. 49B). Their axes are slightly thickened (fig. 49A) as is common in true heads (cephalia). Below the proximal florets, sterile bracts may be present, which in *B. ecklonii* are larger than the leaves and form a small involucre (fig. 49Cf4). As the proximal flowers are often inhibited, it is possible that these bracts are not in fact sterile, but represent the subtending bracts of inhibited floret primordia.

Figure 49C shows leaf metamorphosis in the species analyzed. As a general trend the length of the simple leaves (fig. 49C1,2) decreases from the proximal to the distal part of the shoot. In some species, e.g. *B. lanuginosa*, *B. abrotanoides*, *B. burchellii* or *B. incurva* (fig. 49Ca,c,i,h), the decrease is gradual, while in other species, especially in *B. arachnoidea* and *B. rubra* (fig. 49Cj,k), leaf size changes abruptly. The greatest difference is evident between the foliage of the main axis and the bracts at the base of the flowering short-shoots (fig. 49C2,3) indicating the short-lived nature of these shoots, which are shed after seed set. The flower-subtending bracts and prophylls (fig. 49C5,6) usually increase in length again. They appear to protect the buds, being often curved and hirsute.

A characteristic feature of the genus *Berzelia* (though not present in all species) has been found in *B. lanuginosa*, *B. abrotanoides*, *B. galpinii* and *B. intermedia*. At the base of the uppermost flowering short-shoots brilliant red "cushions" develop; these are most conspicuous in the prefloral (fig. 41A) and postfloral phase (fig. 15B), when they are not hidden by the flowering pincushions (as e.g. in fig. 21b, 36D, 47). Their function is unknown; Boucher (pers. comm.) suggests a myrmecochorous role. Anatomically they comprise massive homogenous tissues. It is not known whether they are induced by fungi or insects (like galls) or not. Their position and the occasionally bilobed appearance may indicate that they are homologous with leaf base structures.

Summary. Figure 50 illustrates the branching and flowering patterns of the genus *Berzelia* in a generalized way. Regardless of the fact that the apex usually continues to grow on for several seasons, the reference system (RS) (fig. 50A) is for reasons of comparison shown as a sympodial unit (SU).

All species of the genus agree in having numerous inflorescences arranged in compound patterns. To describe the complexity clear terms are necessary; these are summarized below:

The reference system (RS) is defined as a flowering sympodial unit which develops in one season (SU = SGU). It is subdivided into an apical zone (az) which in *Berzelia* always remains vegetative, a renewal zone (rz) and a branching zone (bz). In *Berzelia* all flowering short-shoots are part of the branching zone. As they are aggregated within the distal part, the branching zone may be further subdivided into a distal flowering zone (fz) and a proximal vegetative zone (vz). The flowering zone is formed by several aggregates of inflorescences, the terminal one (tia) and lateral aggregates of different orders of branching (lia', lia''). The term 'aggregate of inflorescences' is strictly descriptive, meaning any part of the flowering zone which is separated from other parts by foliage, homogenization or any other means. The individual inflorescences which in *Berzelia* function as pincushion-blossoms are

arranged within the aggregates on branches of different order (I-III). Flowering lateral shoots ending in an inflorescence are termed determinate lateral shoots (dL) while those only having lateral inflorescences are termed indeterminate lateral shoots (iL). As the RS shows, the subdivision of the branching zone into a flowering and a vegetative zone is not clear-cut: sylleptic vegetative lateral shoots (svL) may appear within or among the inflorescence aggregates and sylleptic flowering lateral shoots (sfL) within the vegetative zone.

Figures 50B-E illustrate the variety of the RS. Monopodial connections (B: mc) of individual SGUs are very common in the genus. Basitony (D: ba) within the flowering zone results in a corymbose pattern while homogenization (D: *H*) and disjunction (D: *D*) form racemose patterns. The number and position of the sylleptic vegetative lateral shoots (E: svL) is variable as is the number of the sylleptic flowering lateral shoots (sfL), the aggregates of inflorescences and the inflorescences themselves. The position of the renewal shoots changes only rarely. As fig. 50C shows, indeterminate lateral shoots (α, β) or vegetative lateral shoots within (χ) or below (δ, ε) the flowering zone occasionally function as renewal shoots.

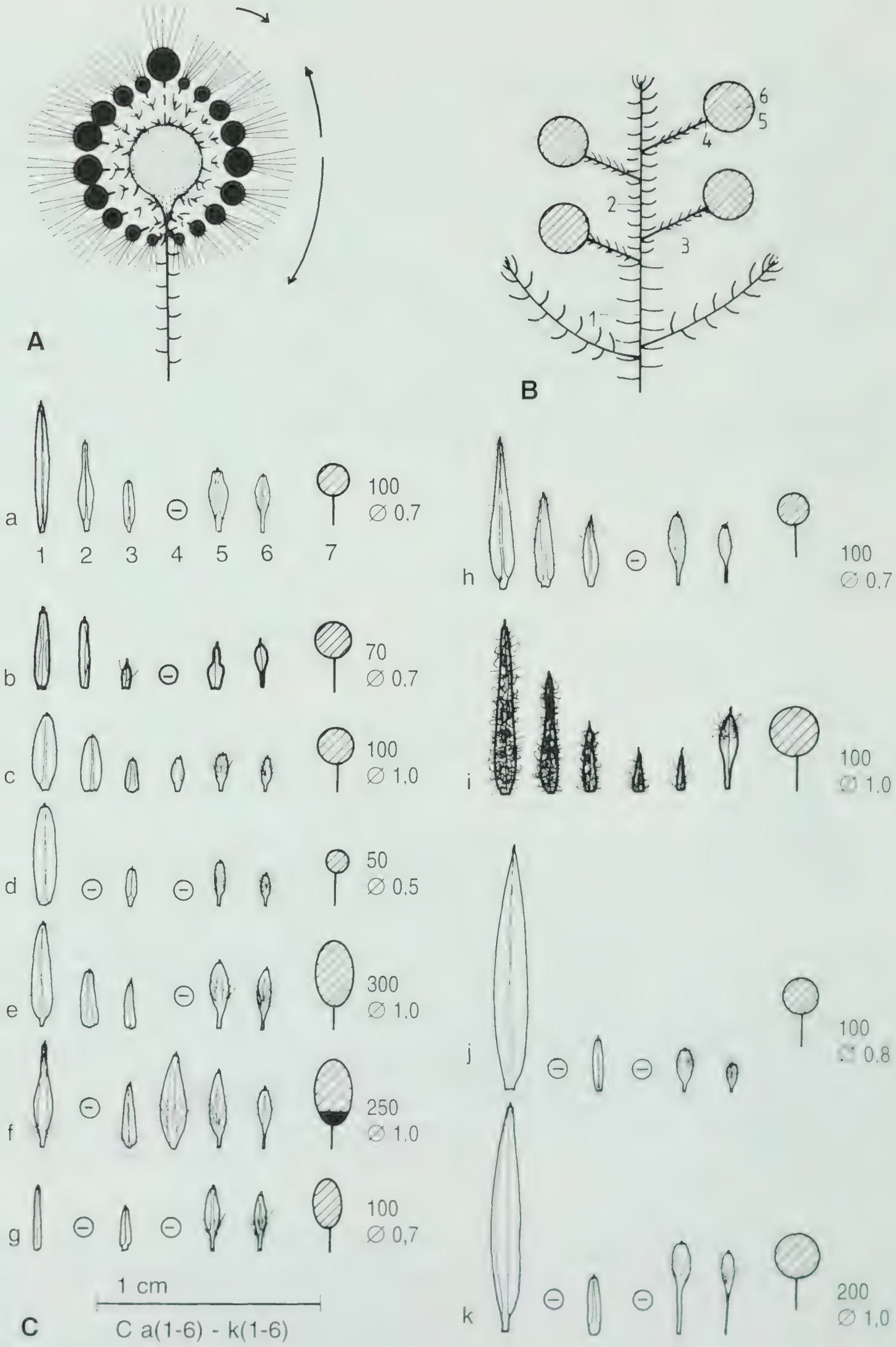


Figure 49 - **Berzelia:** ***Leaf metamorphosis and inflorescence structure****. A, profile of an inflorescence showing the pincushion-like habit, the terminal flower, the flower-subtending bracts and prophylls and the flowering sequence (arrows), B, profile of a flowering shoot showing the lateral arrangement of the inflorescences and leaf metamorphosis, C, leaf metamorphosis of the species analyzed: 1, foliage, 2,3, leaves and bracts among the flowering short-shoots (2) and below the inflorescences (3), 4, sterile bract below the proximal florets, 5 flower-subtending bract, 6 prophyll; a,* B. lanuginosa, *b,* B. *spec, c,* B. abrotanoides, *d,* B. commutata, *e,* B galpinii, *f,* B. ecklonii, *g,* B. intermedia, *h,* B. incurva, *i,* B. burchellii., *j,* B. arachnoidea, *k,* B. rubra.

the numbers 1-6 in B correspond to the numbers 1-6 in C, the numbers in C7 represent the average number of florets per inflorescence and, below, the diameter of the inflorescences in cm

Black in Cf7: involucre

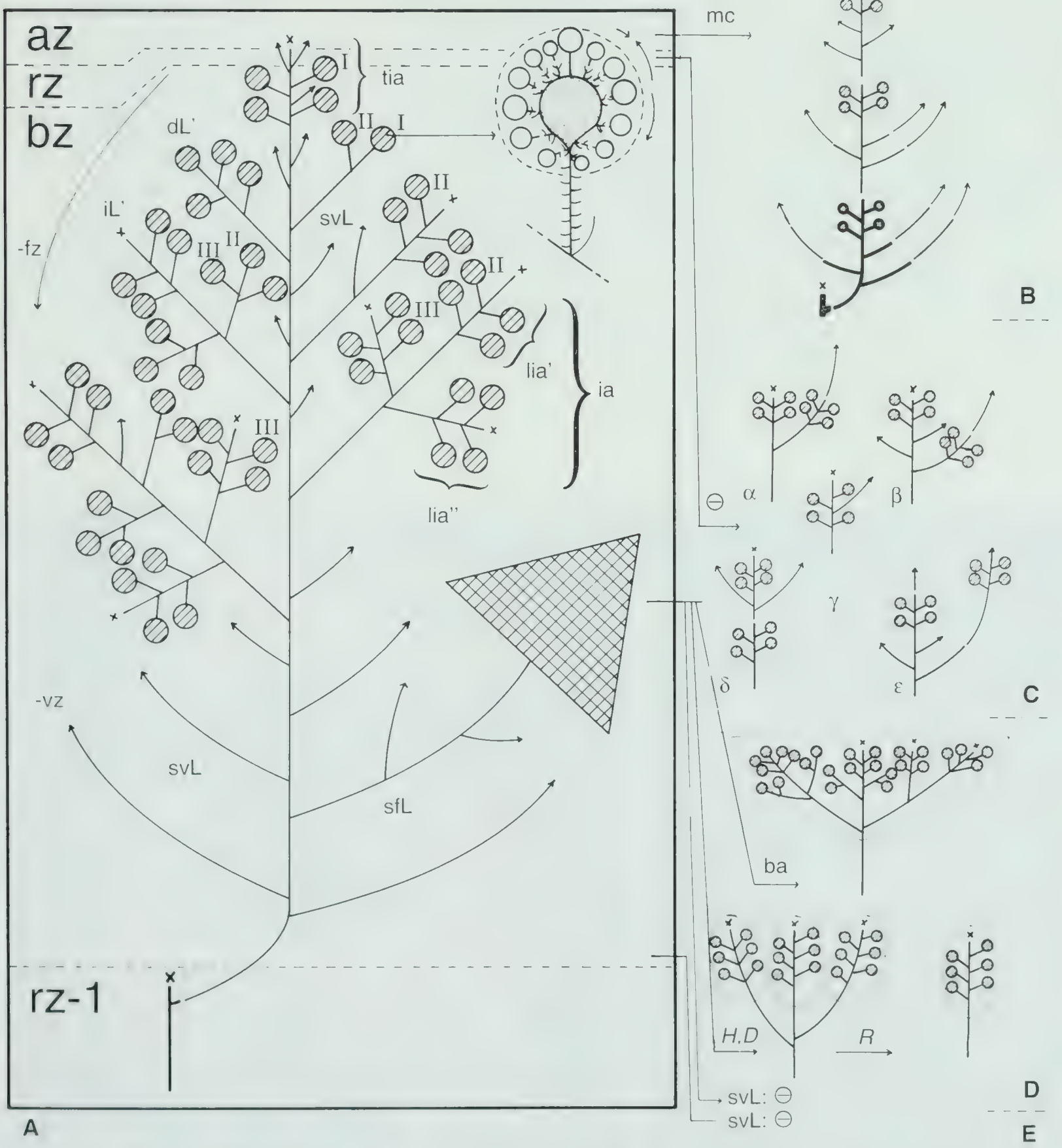


Figure 50 - ***Model of the genus*** **Berzelia**. *A, reference system (RS): the apex dies off, the renewal zone is always above the inflorescence cluster, which is part of the branching zone and composed of numerous pincushion-like cephalia. B-E, variations of the RS as regards the behaviour of the apex (B), the position of the renewal shoots (C), the arrangement of the inflorescences (D) and the appearance of sylleptic vegetative lateral shoots (E).* ba, *basitony,* D, *disjunction,* ia, *aggregate of inflorescences ,* R, *reduction.*

3.3 ***Brunia*** Lam.

The genus has seven species. B. albiflora *and* B. nodiflora *are common, while* B.macrocephala *is cited as rare (Hilton-Taylor 1996). The other species show a scattered distribution but are locally frequent. A natural hybrid,* B. albiflora *x* B. stokoei, *is known and is cultivated at the nursery of the National Botanic Garden Kirstenbosch.*

B. nodiflora *and* B. albiflora *were studied at various localities in the Western Cape Province,* B. stokoei *at Kogelberg Nature Reserve and above Betty's Bay,* B. alopecuroides *at Mount Lebanon and at Landrostkop,* B. laevis *at Houw Hoek and near Bredasdorp and* B. neglecta *above Hermanus.* B. macrocephala *was analyzed from herbarium specimens.*

The two genera Berzelia *and* Brunia *are very similar. They have been distinguished at the bases of a different number of ovary locules (e.g. Pillans 1947; compare with fig. 4), but this character has proved to be too variable to distinguish separate genera.*

Figure 51 - **Brunia nodiflora**. *A,B, shrubs at Karbonkelberg (near Cape Town, A) and at Elandsberg (Ladismith, B) in the prefloral stage, showing the conspicous silvery buds of the inflorescences and the large persistent postanthetic inflorescences, C, a plant cultivated in the Botanic Garden Kirstenbosch, showing the characteristic vegetative habit of the SGUs with dominant main axes and many, relatively short lateral shoots.*

Growth and branching pattern. All species of the genus are erect shrubs 60-90 cm in height (*B. nodiflora, B. neglecta, B. laevis, B. macrocephala*) or up to 2-3 m (*B. alopecuroides, B. albiflora, B. stokoei*). Though all species bear conspicuous pincushion-like inflorescences, there are clear differences between individual species:

The most remarkable characteristics of *B. nodiflora* (fig. 51) are its high vegetative vitality, the silvery buds of its inflorescences and the persistence of its large deflorated inflorescences for about three years (Nel 1986). A further characteristic feature, more clearly shown in figures 52-54, is the premature development of the next season's shoots (n+1) by means of the main axis growing on (mc) or the renewal shoots (R) sprouting, when the current inflorescences (n) are still flowering. Usually the SGU of the Bruniaceae is characterized by a developmental regime that begins with the formation of vegetative shoots and ends with anthesis of flowers which are formed in exactly the same season (compare with fig. 14). Compared with this standard situation, the shoot system of *B. nodiflora* differs in not completing its whole developmental regime in one season, but postponing anthesis of the flowers into the next season, or in other words: it differs in growing vegetatively during the first season and flowering in the second. This appears to result from superposition of the developmental programmes of two SGUs and the synchronisation of the vegetative stage of season n+1 with the flowering stage of season n.

Interpreting the time-shift as a variation of the standard situation, the SGU of *B. nodiflora* can be directly compared with the shoot systems of the remaining members of Bruniaceae. The SGU, then, may be subdivided into a proximal vegetative zone (fig. 52: vz) with sylleptic vegetative shoots (fig. 52-54: svL) and a distal flowering zone (fig. 52: fz) with sylleptic flowering shoots (fig. 52-54: sfL). These zones are very clear in young plants or rejuvenated shoot systems (fig. 52) while older plants tend to have more enlarged flowering zones interspersed with vegetative shoots, and only small or even no entirely vegetative zones (fig. 53).

The individual SGUs are connected in a monopodial or in a sympodial manner. Besides the main axis, the vegetative and flowering lateral shoots are also capable of continuing to grow on (fig. 53, 54: mc') or to form renewal shoots (R) so that a high potential for lateral branching exists whereby the shoot system may be continued after the main axis dies off or terminates in an inflorescence.

A terminal inflorescence may be present (fig. 53: arrows) or absent (fig. 52). The flowering zone may be composed of only lateral unbranched shoots of the 1st order (sfL) each of which increases in length from distal to proximal zone and ends in a terminal inflorescence (fig. 52) or may be much-branched, showing inflorescences of 2nd and even 3rd order (fig. 53, 54: II,III). In this case, the order of branches and inflorescences and the number of vegetative branches do not increase gradually from distal to proximal zone but reach a maximum in the medial part (fig. 53, 54: iL'). The lateral flowering shoots usually end in a terminal inflorescence (fig. 53, 54: dL), but very strong shoots are indeterminate (iL) and continue to grow on (mc') as may the main axis of the shoot system. The flowering shoots of 2nd order (II) always are determinate. They may be branched, and have either unbranched flowering shoots of 3rd order (III) or vegetative shoots.

Vegetative shoots appear at various positions within the flowering zone (fig. 53): on the main axis among the flowering shoots as much-branched shoot systems (a), at the base of the flowering shoots of 1st order, repeating there the zones of the main axis (b), as short, often unbranched shoots of 1st to 3rd order of branches among the corresponding flowering shoots (c), as renewal shoots below any terminal inflorescence (d).

B. neglecta and *B. laevis* are similar to *B. nodiflora* in respect of height, branching pattern, foliage, arrangement and size of the inflorescences, but differ in lacking the premature development of the next season's shoots.

The SGUs of *B. neglecta* (fig. 55B) are characterized by a richly branched vegetative zone and a large terminal flowering zone (fig. 56: vz, fz). Occasionally a terminal inflorescence is present (fig. 57B ti), but usually the apex of the main axis remains vegetative, growing on in the next season (fig. 56: mc) or dying off (fig. 56, 57). The lateral inflorescences ranging from 1st to 3rd order of branches (I-III) are arranged in a conjunct pattern (fig. 57A,B), but this general tendency does not exclude weaker shoots in the proximal part of the flowering zone (fig. 57B). The flowering shoots of 1st order are determinate (fig. 57A,B: dL') or indeterminate (fig. 56: iL'), the whole cluster of inflorescences is interspersed with

vegetative shoots. The individual SGUs are connected in a monopodial (fig. 56: mc) or sympodial manner which is very extreme in the example shown in figure 57A,A′.

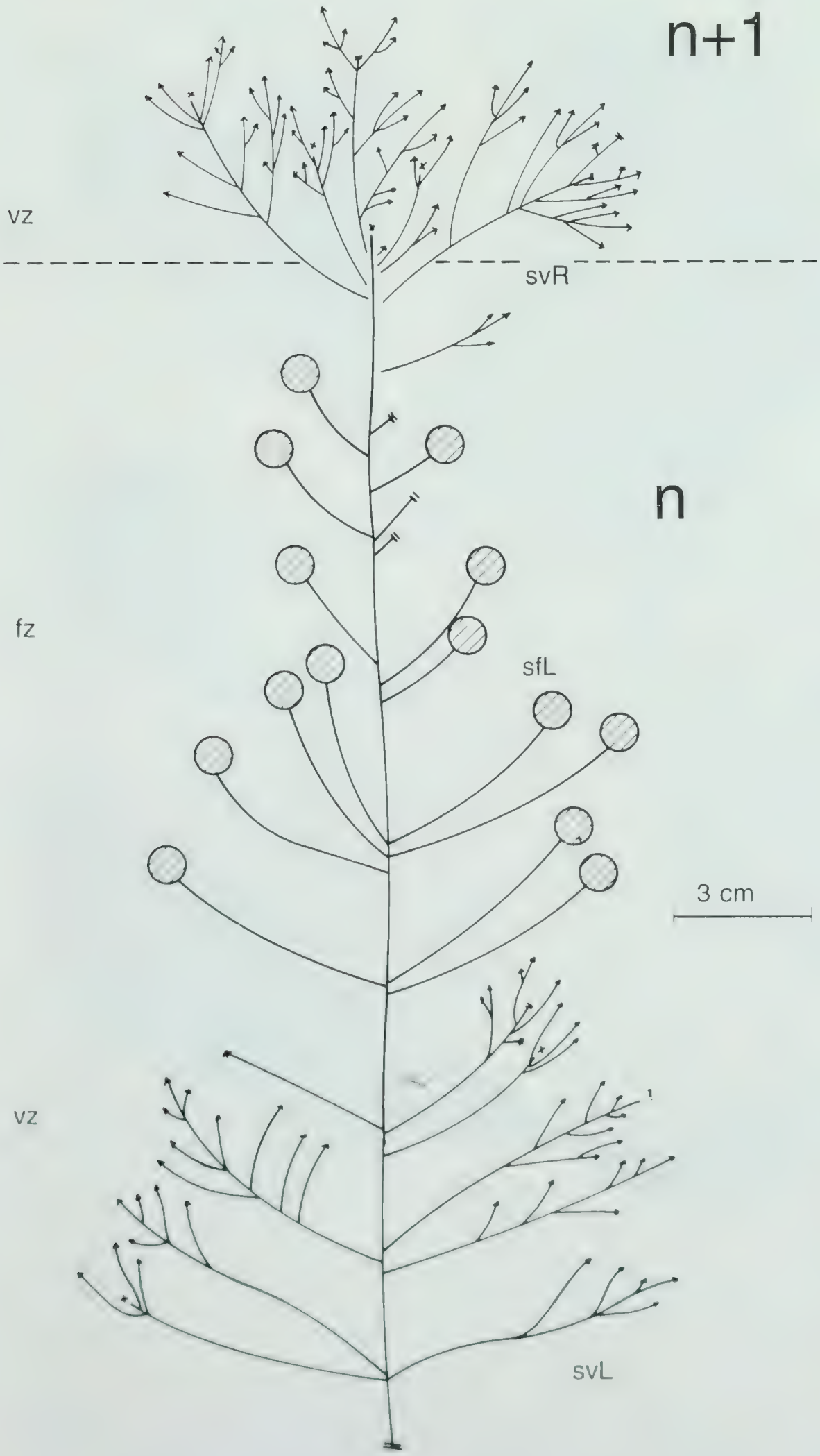


*Figure 52 - **Brunia nodiflora**. Profile of a flowering shoot system. The inflorescences terminate short lateral shoots which are arranged in groups of three to five at the main axis. While flowering, renewal shoots commence growth above the cluster of inflorescences.*

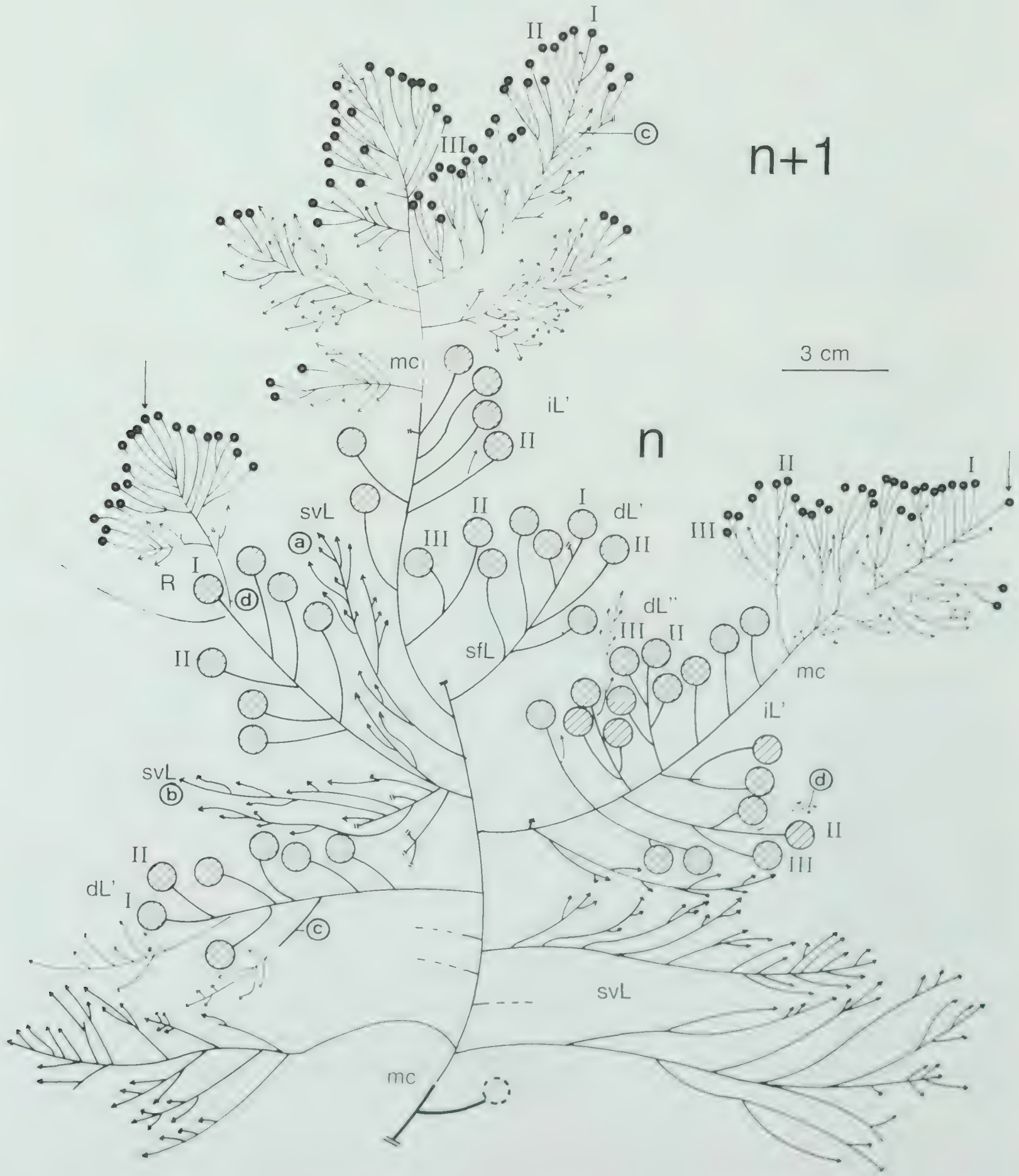


Figure 53 - **Brunia nodiflora**. *Profile of a flowering shoot system. During flowering, the buds (black) of the next season's inflorescences* (n+1) *are already present. Note the occasional presence of a terminal inflorescence (arrow), the different order of flowering branches* (I-III) *and the different types of vegetative lateral shoots.* *a-d, compare with text (p. 72)*

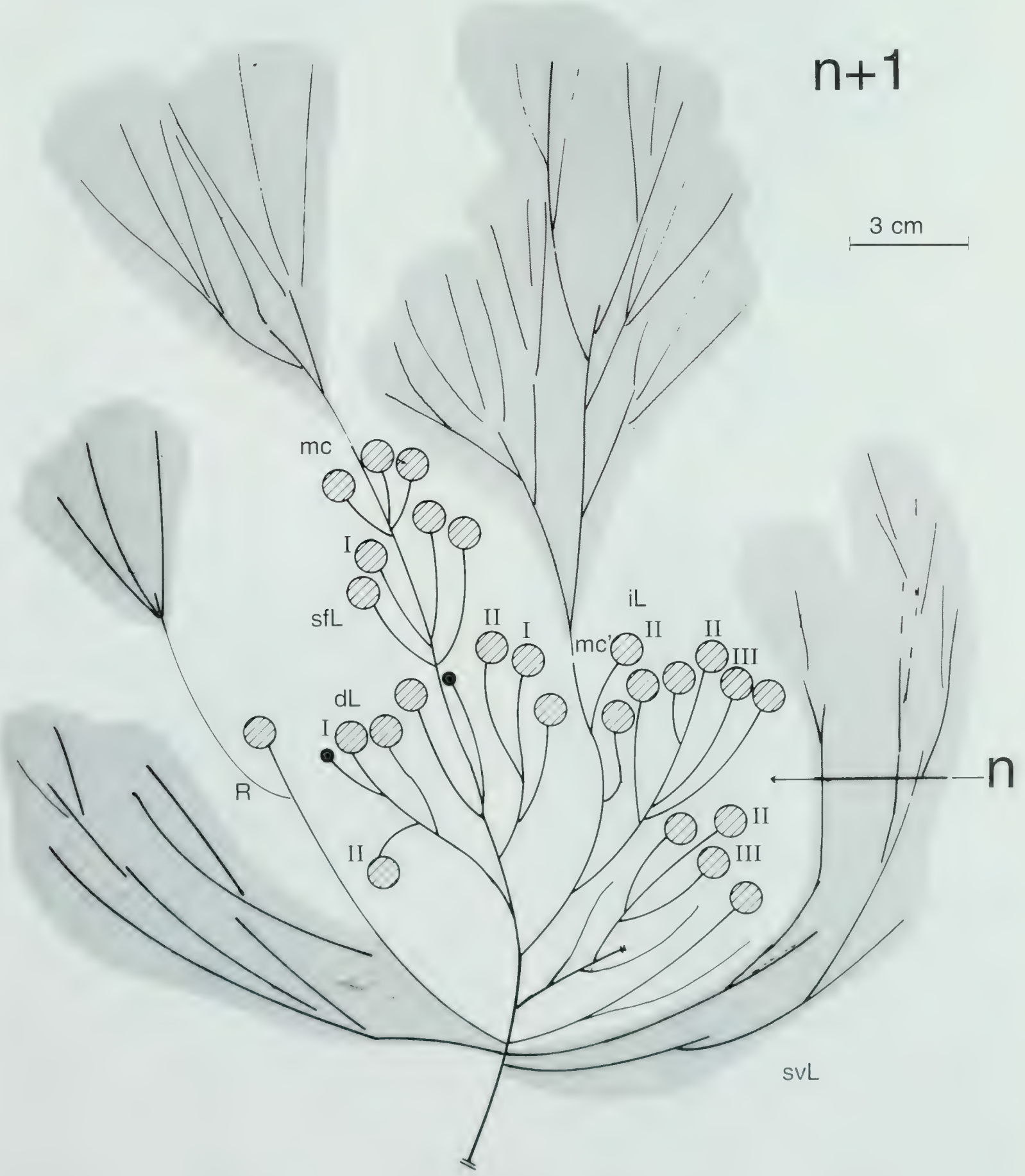


Figure 54 - **Brunia nodiflora**. *Profile of a flowering shoot system, the vegetative lateral shoots and renewal shoots only being outlined. Note the growing on of the main axis* (mc) *and of the indeterminate lateral shoot* (mc') *and the renewal shoot* (R) *below the terminal inflorescence of the determinate lateral shoot.*

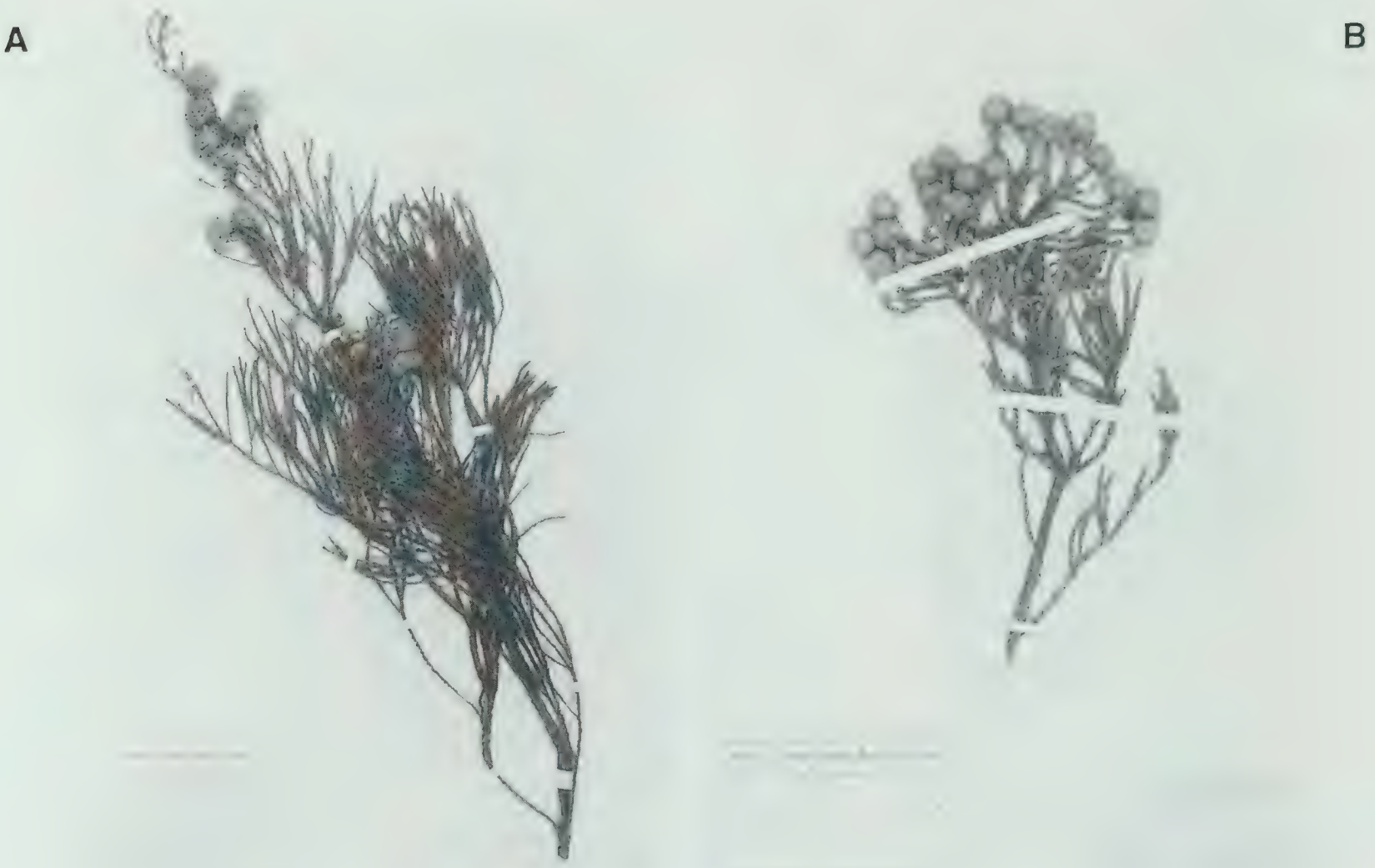


Figure 55 - ***Flowering shoots systems in the genus*** **Brunia**. *A*, B. nodiflora (Berzelia nodiflora, *Bayliss 270, B*), *B*, B. neglecta *(Schlechter 7297, B)*, *C*, B. macrocephala *(Schlechter 2283, B)*, *D*, B. alopecuroides *(Werdermann & Oberdieck 214, B)*.

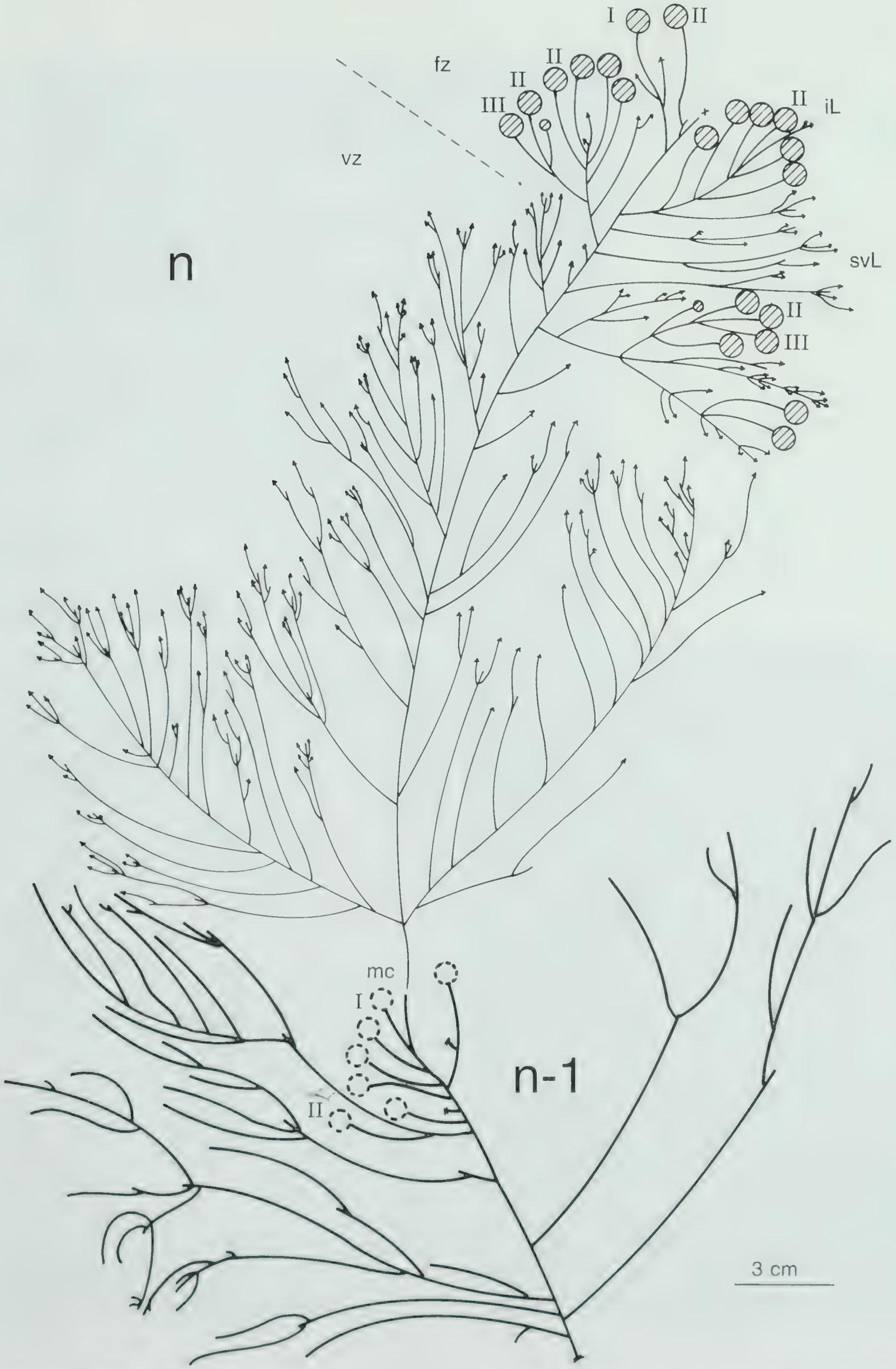


Figure 56 - **Brunia neglecta**. *Profile of a flowering shoot system, representing two seasons' growth, showing the indeterminate cluster of inflorescences* (I-III), *extensive branching along the whole main axis and occasional monopodial connection* (mc) *of two SGUs* .

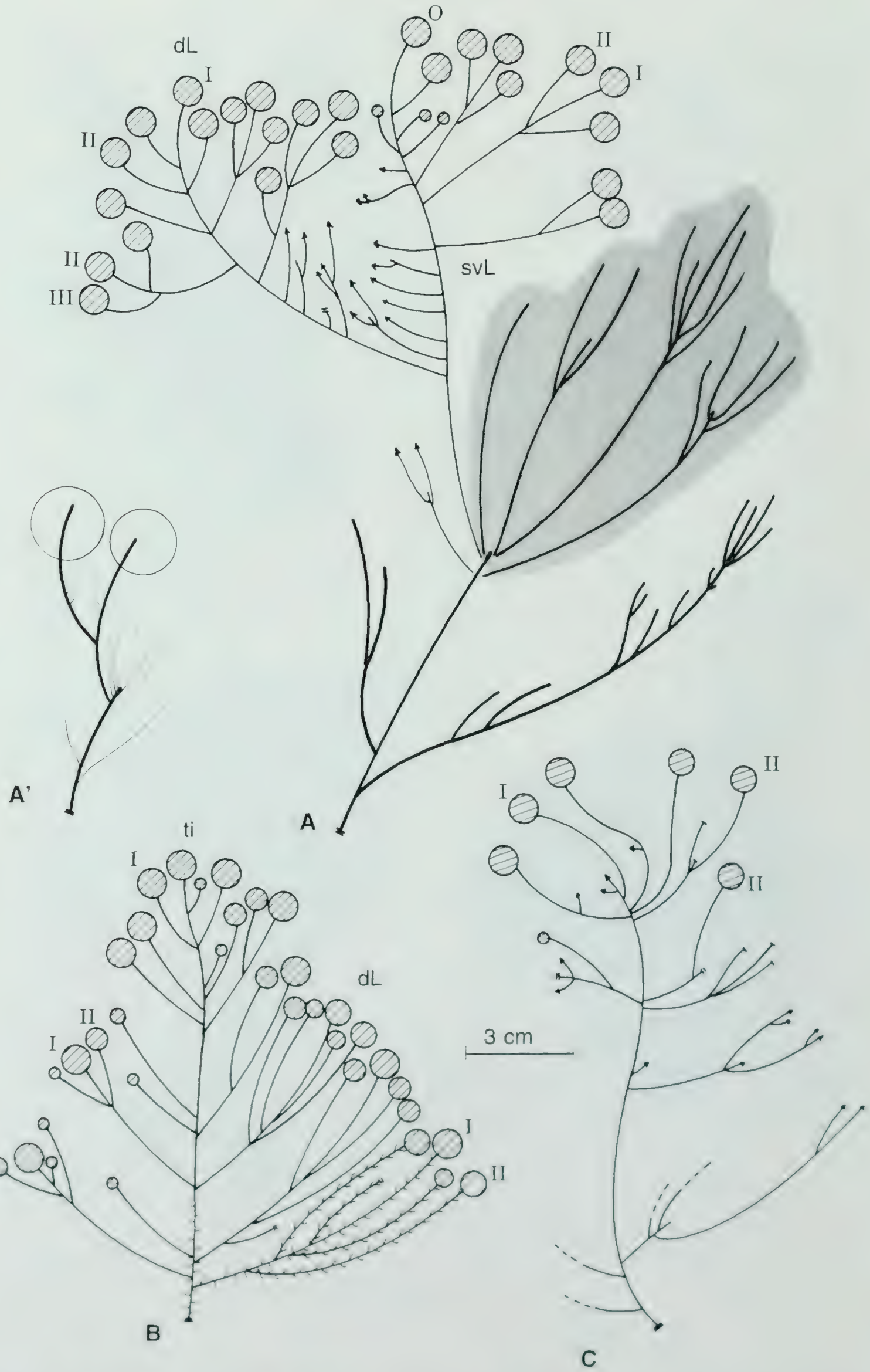


Figure 57 - **Brunia neglecta**. *Flowering shoot systems: A, A', profile (A) and habit (A', schematically) of a shoot system showing a lateral cluster of inflorescences, B, a terminal, conjunct cluster of inflorescences with a terminal inflorescence* (ti) *and determinate lateral shoots only* (dL)

Figure 58 - **Brunia laevis**. *A, a shrub in the prefloral stage with large persistent, postanthetic inflorescences, coastal fynbos at Soetanysberg near Bredasdorp. B,C, plants being cultivated at the nursery of the Botanic Garden Kirstenbosch, showing the variable branching patterns.*

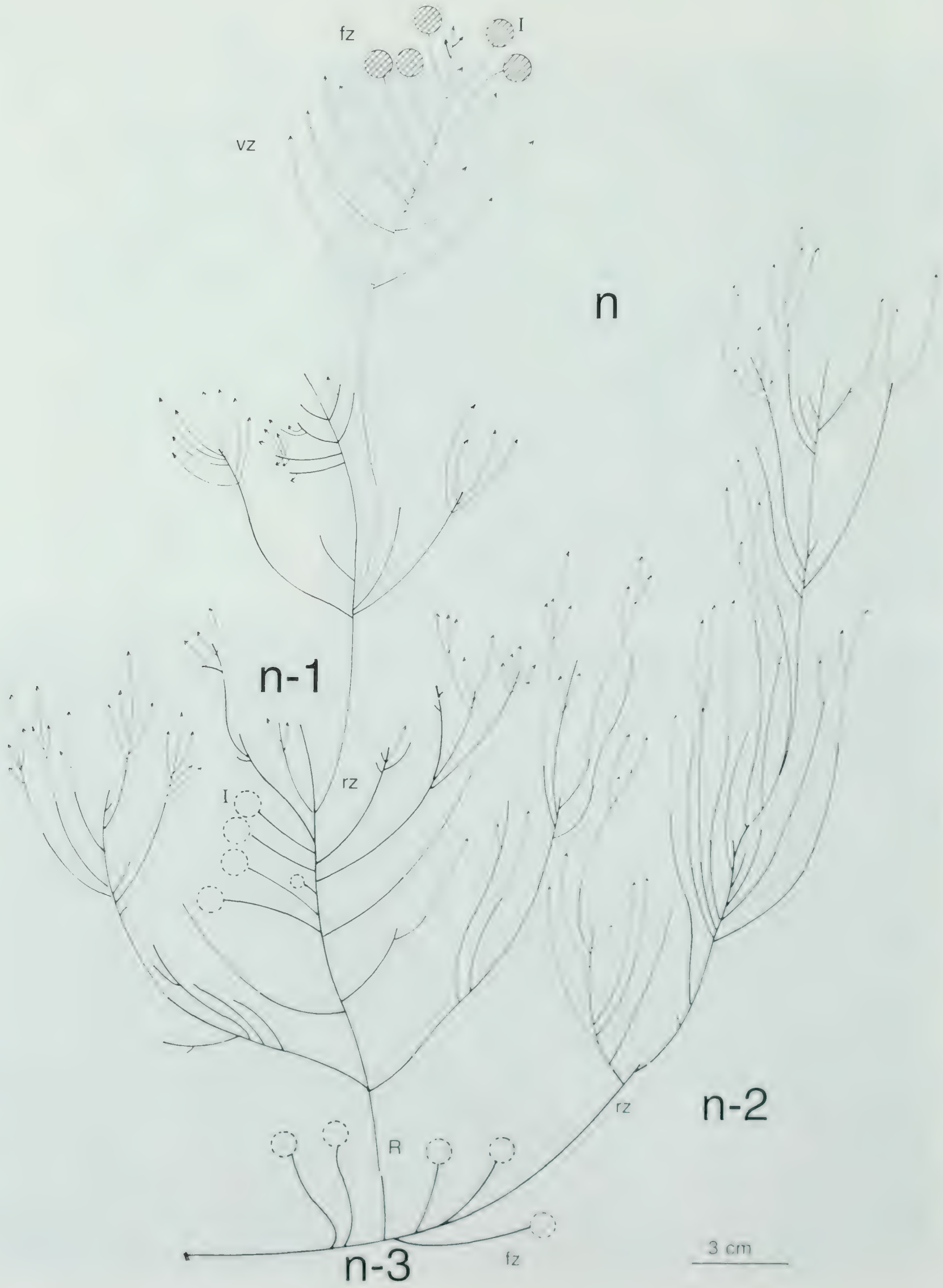


Figure 59 - **Brunia laevis**. *Profile of a shoot system, representing four seasons' growth, showing renewal zones both above (*rz*) and within the inflorescences (*R *). Note the insertion of the vegetative SGU in season n-1.*

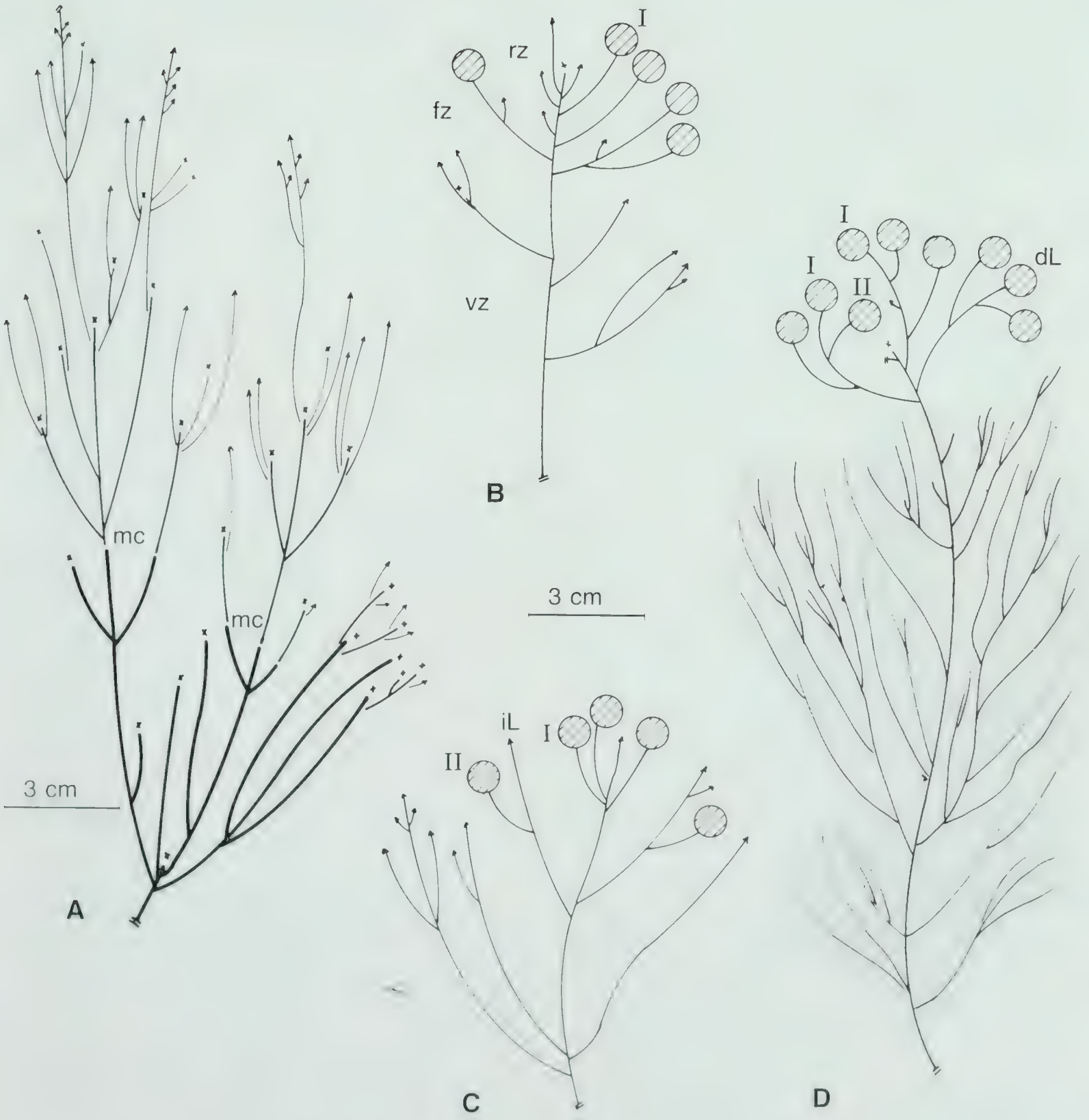


Figure 60 - **Brunia laevis**. *Profiles of shoot systems. A, juvenile, not yet flowering shoot system, four seasons old, with occasional monopodial connections between two SGUs, B-D, flowering shoot systems showing the variation of the flowering zone.*

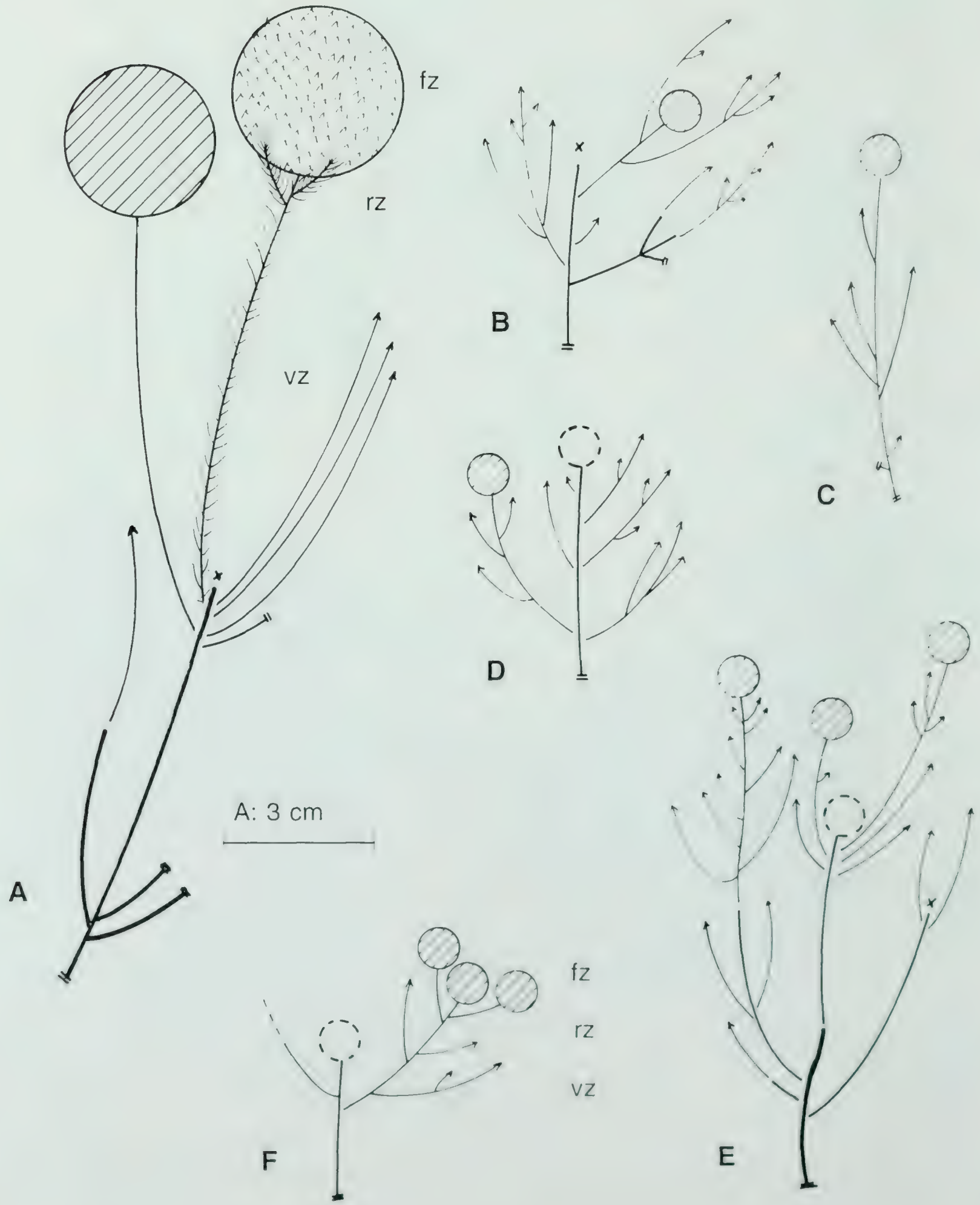


Figure 61 - **Brunia macrocephala**. *A-F, profiles of flowering shoot systems. Note the large, usually solitary terminal inflorescence and the subfloral renewal zone below.*

The SGUs of *B. laevis* (fig. 58) are subdivided into a proximal vegetative zone with mainly unbranched lateral shoots, a flowering zone and a distal renewal zone (fig. 59, 60B). The flowering zone is manifold: it is either composed of unbranched flowering shoots (fig. 59: I) or of branched determinate (fig. 60D: dL) or indeterminate (fig. 60C: iL) lateral shoots with inflorescences of 1st and 2nd (I,II) or of 2nd order (II) only. Monopodial connection of individual SGUs has been found only in juvenile shoot systems which have not yet flowered (fig. 60A: mc). The flowering shoot systems analysed did not show any terminal inflorescence nor any main axis growing on. Thus, it is expected that the apex of the main shoot may regularly die off at the end of each season. Sylleptic vegetative lateral shoots occur within the flowering zone and occasionally become renewal shoots (fig. 59: R), but usually the shoot system is extended by renewal shoots arising above the flowering zone (fig. 59, 60B: rz). As it is illustrated in fig. 59, within an adult plant each SGU does not necessarily come to flower, but may remain in the vegetative state.

Comparing the two species with *B. nodiflora, B. neglecta* shows the same facultative presence of a terminal inflorescence and *B. laevis* the same distal position of the renewal zone above the flowering zone.

B. macrocephala (fig. 55C, 61) differs from all the remaining species of *Brunia* in having only a few, large (up to 2,5 cm in diameter) inflorescences, the largest simple inflorescences of the whole family. The inflorescences are most often arranged solitarily in a terminal position (fig. 61A-E), but occasionally some lateral flowering shoots of the 1st order (fig. 61F) appear. The vegetative zone of the SGUs is usually branched, the renewal shoots arise below the terminal inflorescence (fig. 61A: rz).

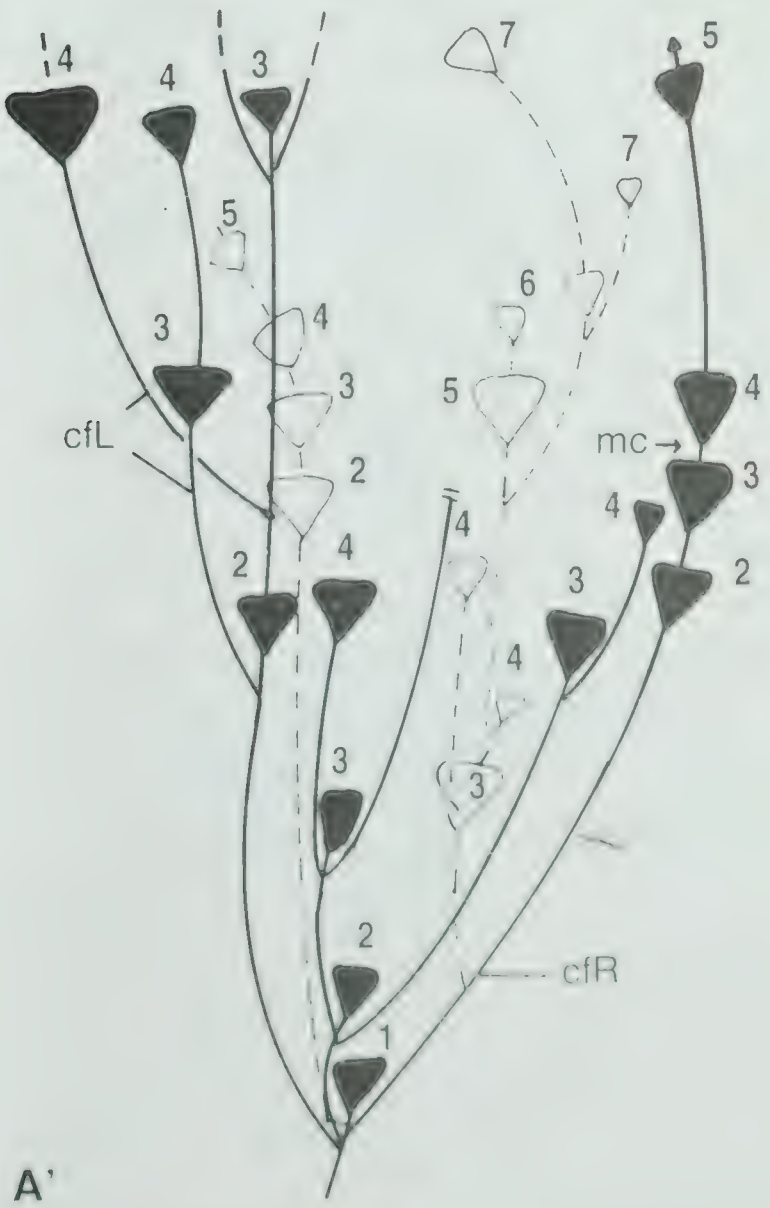
B. stokoei and especially *B. albiflora* and *B. alopecuroides* are tall shrubs of about 1,5 m and 2-3 m in height.

The unique habit of *B. albiflora* is characterized by a few thin stems, a large canopy (fig. 62A) and corymbose clusters of spherical inflorescences (fig. 62B,C), which latter are persistent and, because of repeated monopodial connections, arranged in tiers round the dominant shoot (fig. 62B). Figure 63A shows the middle section of a plant about 3 m in height. This part is leafless and bears numerous old inflorescences from at least seven previous seasons (fig. 63A´: 1-7). As the plants senesce after about ten or twelve years (Dyer 1944: 928) this example obviously shows an old plant. In contrast, the shrub shown in fig. 62C,D and 63B,B´ is much younger. It is about two meters high, covered with spread needle-like leaves and inflorescences representing only three different seasons. The inflorescences of the present season are in an early postfloral stage (fig. 62C,D) and have lost the conspicuous pincushion-like appearance resulting from the numerous stamens exserted at anthesis.

The individual SGU of *B. albiflora* (fig. 64) is clearly subdivided into a proximal vegetative and a distal flowering zone (vz, fz). The vegetative lateral shoots are long, scarcely branched and oriented horizontally. They may continue to grow on and to produce inflorescences for several seasons (fig. 63A´). The flowering shoots are short, mainly unbranched and arranged in terminal flat clusters (fig. 62A). The apex of the dominant shoot continues to grow on, protruding through the terminal cluster of inflorescences (fig. 62C) so that the flowering shoots become clustered round the dominant shoot (fig. 62B). Depending on the length of individual SGUs, the clusters follow in a more or less dense series. After up to four seasons (fig. 63A´) the apex dies off and lateral shoots (mainly from the vegetative zone) renew the shoot system (fig. 66A,B).

Only occasionally does the SGU differ from this typical form. Very rarely, an inflorescence may terminate the dominant shoot (fig. 62D) or the flowering zone be composed of unbranched and additional branched shoots (fig. 65). The branched shoots are arranged below the distal ones and bear inflorescences of 2nd order. They are determinate (dL), ending in a terminal inflorescence of 1st order or indeterminate (iL), having inflorescences of 2nd order only. The apex then dies off or continues to grow on (mc´). Vegetative shoots may appear within the flowering zone (fig. 65n-1: svL). Renewal shoots arise mainly from the vegetative zone (fig. 66A,B), but may also appear above the cluster of inflorescences (fig. 65n-1: R, 66C) or as indeterminate lateral shoots (fig. 66E). In a single case a renewal shoot was found arising as a shoot of 2nd order from a lateral determinate flowering shoot (fig. 65n: R, 66D)

Figure 62 - **Brunia albiflora**. *A, characteristic growth form of a shrub at Kirstenbosch Botanic Garden showing the few thin stems and the branched canopy, B-D, flowering shoot systems in the postfloral stage. Note the annular arrangement of the inflorescences round the main axis, the continuation of the shoot system by onward growth of the apex of the main axis in the next season (C), the resulting monopodial connection of the SGUs (B) and the very rare appearance of a terminal inflorescence (D).* *C,D: details of fig. 63B*



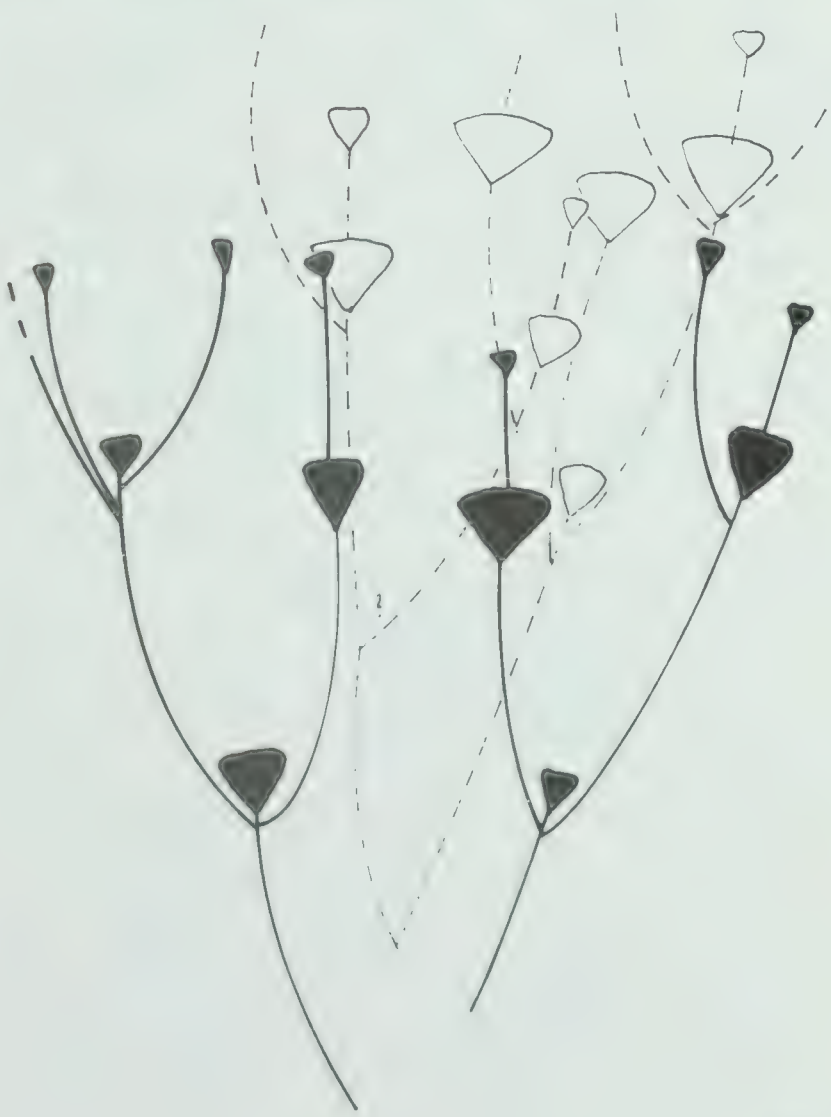


Figure 63 - **Brunia albiflora**. *A, habit of an old shrub at Fairy Glen, the basal part being characterized by leafless branches and deflorated clusters of inflorescences arranged in tiers, B, habit of a younger plant at Kirstenbosch Botanic Garden (compare with fig. 62C,D), A', B', profiles of the shrubs shown in A and B. Note the numerous monopodial connections and the position of the renewal shoots below the terminal cluster of inflorescences.* 1-7 *in A': flowering seasons.*

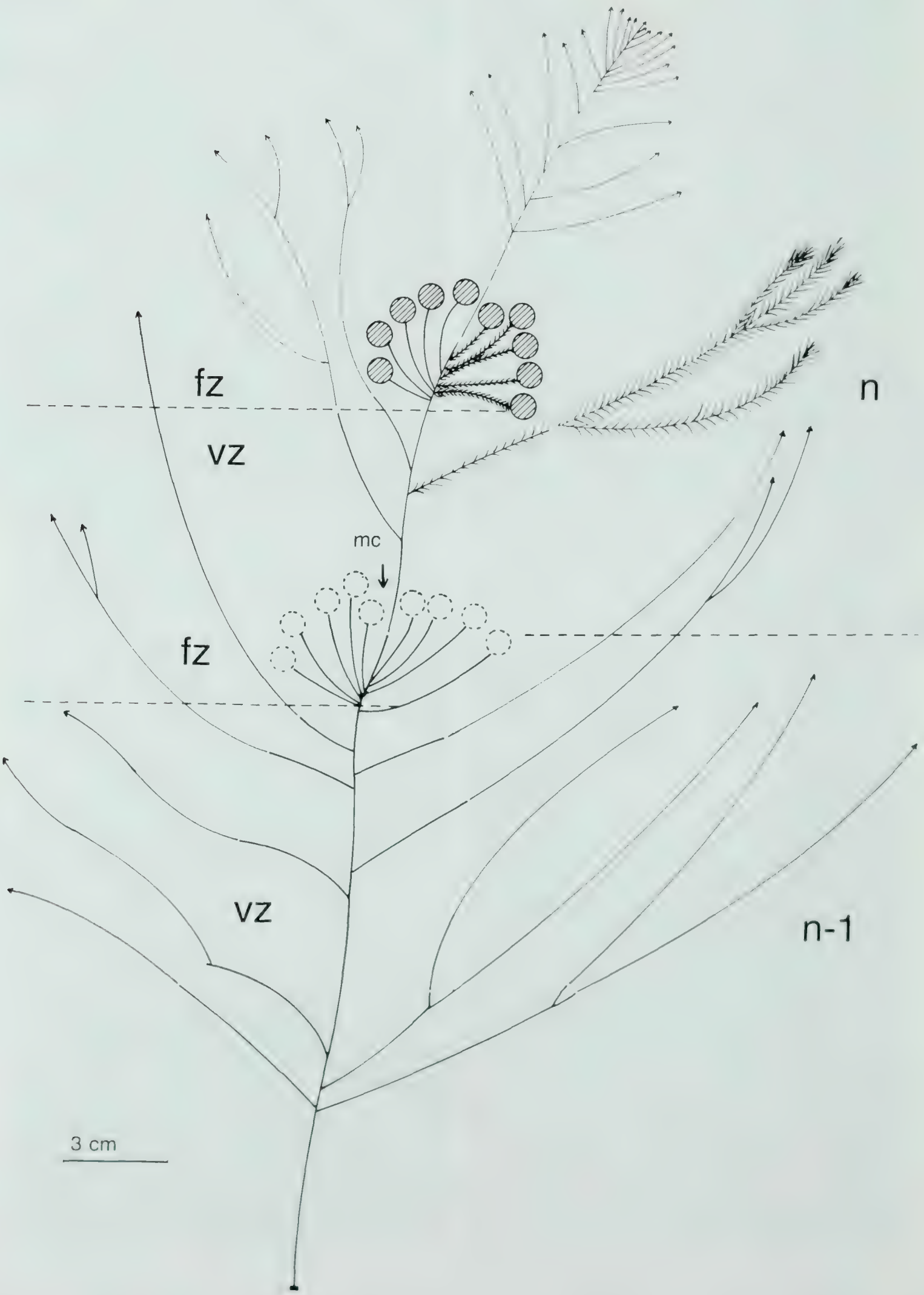


Figure 64 - **Brunia albiflora**. *A, profile of a characteristic flowering shoot system with simple clusters of inflorescences arranged round the main axis and monopodial connections between the individual SGUs.*

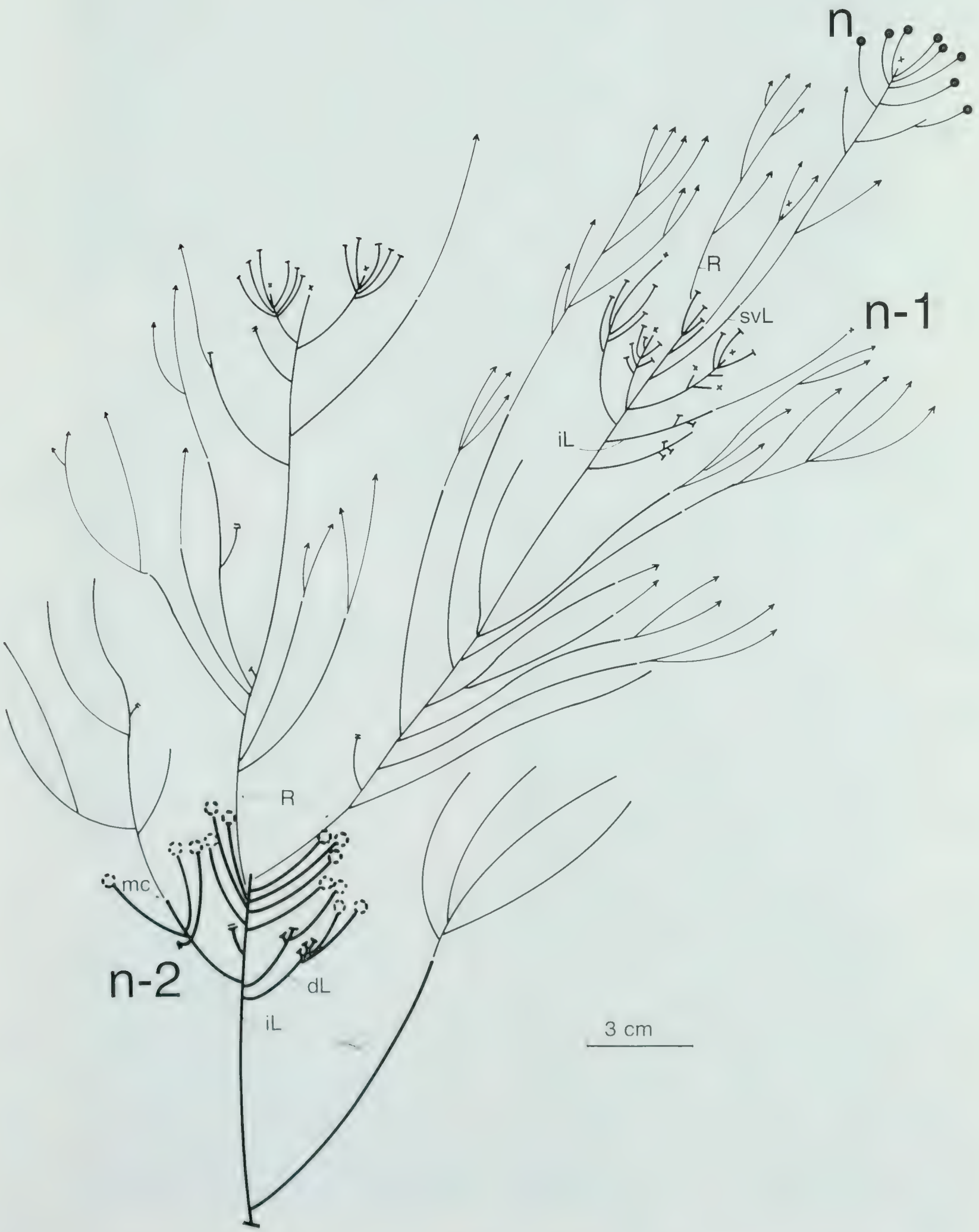


Figure 65 - **Brunia albiflora**. *Profile of a less characteristic flowering shoot system, three seasons old. Note the compound nature of the flowering zone with determinate* (dL) *and indeterminate lateral shoots* (iL), *the inflorescences of 1st* (I) *and 2nd* (II) *order of branches and the subterminal position of some renewal shoots* (R) *above the inflorescences.*

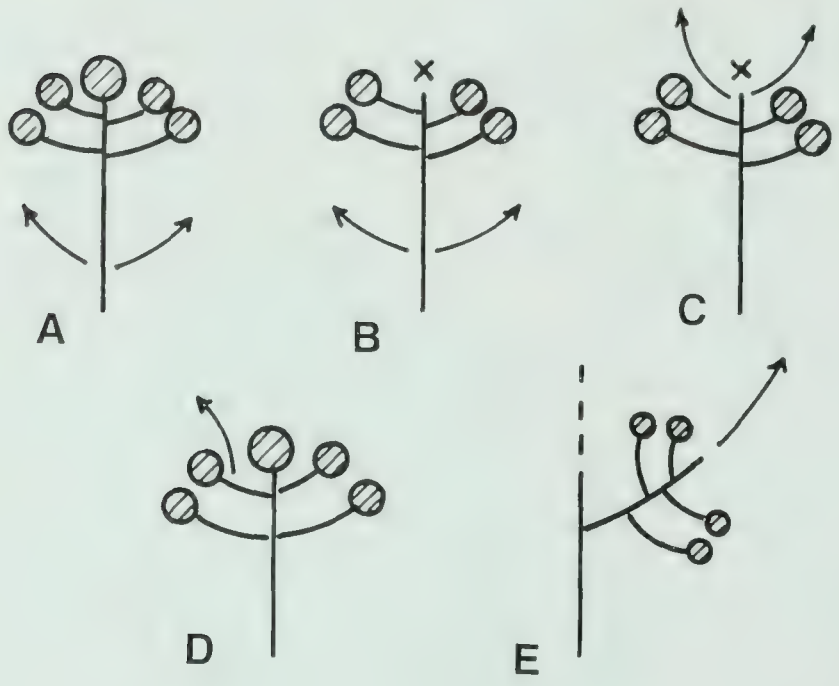


Figure 66 - **Brunia albiflora**. *Position of the renewal shoots: A,B, characteristic position below the flowering zone, C-E, occasional position above the inflorescences (C) and within the flowering zone arising from an indeterminate (E) or very rarely from a determinate lateral shoot (D).*

B. stokoei (fig. 67) resembles *B. albiflora* in having similar flat clusters of inflorescences arranged in tiers and separated by repeated monopodial connections (fig. 68C: mc). The flowering zone is likewise composed of short unbranched shoots only (fig. 68C,D, 69A) or of unbranched and branched shoots which however always appear indeterminate (fig. 68A, 69B: iL). Terminal inflorescences were not found.

The vegetative zones of the individual SGUs often have only a few lateral branches, but, additional, possibly compensatory, vegetative shoots may appear among the flowering shoots (fig. 69A: svL). Where the vegetative zone is completely lacking, strictly reproductive SGUs result. Such shoots are able to grow on terminally and to flower for several seasons (fig. 68C). As there are no primordia of lateral renewal shoots present, the whole shoot system then dies off and must be renewed by vegetative shoots from older parts of the shrub (fig. 68C: n-2).

The SGUs are connected in a mainly monopodial manner. After two (or more ?) seasons the apex of the dominant shoot dies off and the shoot system is continued by renewal shoots. These correspond to indeterminate flowering shoots (fig. 67C, 69B: R) or to vegetative shoots arising from above (fig. 69A) or within the flowering zone, or from the vegetative zone of the same or of an older SGU.

B. alopecuroides (fig. 70) is characterized by large clusters of yellowish inflorescences which become red after anthesis. Each SGU (fig. 72) is subdivided into a proximal, much-branched vegetative zone (vz) and a distal flowering zone (fz), the main axis of which tends to continue its growth in the following season (mc). As most of the (up to twenty) lateral flowering shoots also continue to grow on (mc'), a much-branched system results, with a high capacity for continuation of the shoot system. When the apex of the dominant shoot dies off, numerous vegetative and flowering branches are able to renew the shoot system.

The habit and organisation of the flowering zone are reminiscent of *Berzelia* rather than *Brunia*. The inflorescences terminate bracteate short-shoots and are arranged in a double racemose pattern (fig. 73B). The terminal aggregate of inflorescences, with about 50-60 individual inflorescences, is much larger than the lateral ones, in which the number of inflorescences per aggregate clearly decreases in a distal (20-30) to proximal (1-5) direction (fig. 72, 73B: tia, lia). This numerical decrease is associated with a basipetalous (or centrifugal) flowering sequence, which is accentuated by the fact that the yellowish flowers become red when fruiting (fig. 70B, 71C). Within an individual aggregate, the inflorescences differ in size, but no size gradient may be seen (fig. 73A'). The flowering short-shoots are not as densely aggregated as possible, but are irregularly arranged in groups, and interspersed with sterile bracts (fig. 73A').

Figure 67 - **Brunia stokoei**. *A, habit of a shrub at the Kogelberg Nature Reserve, B, shoot system at the prefloral stage from a plant above Betty's Bay, C, shoot system at the prefloral stage from a plant at Kogelberg Nature Reserve (compare with fig. 69B)*

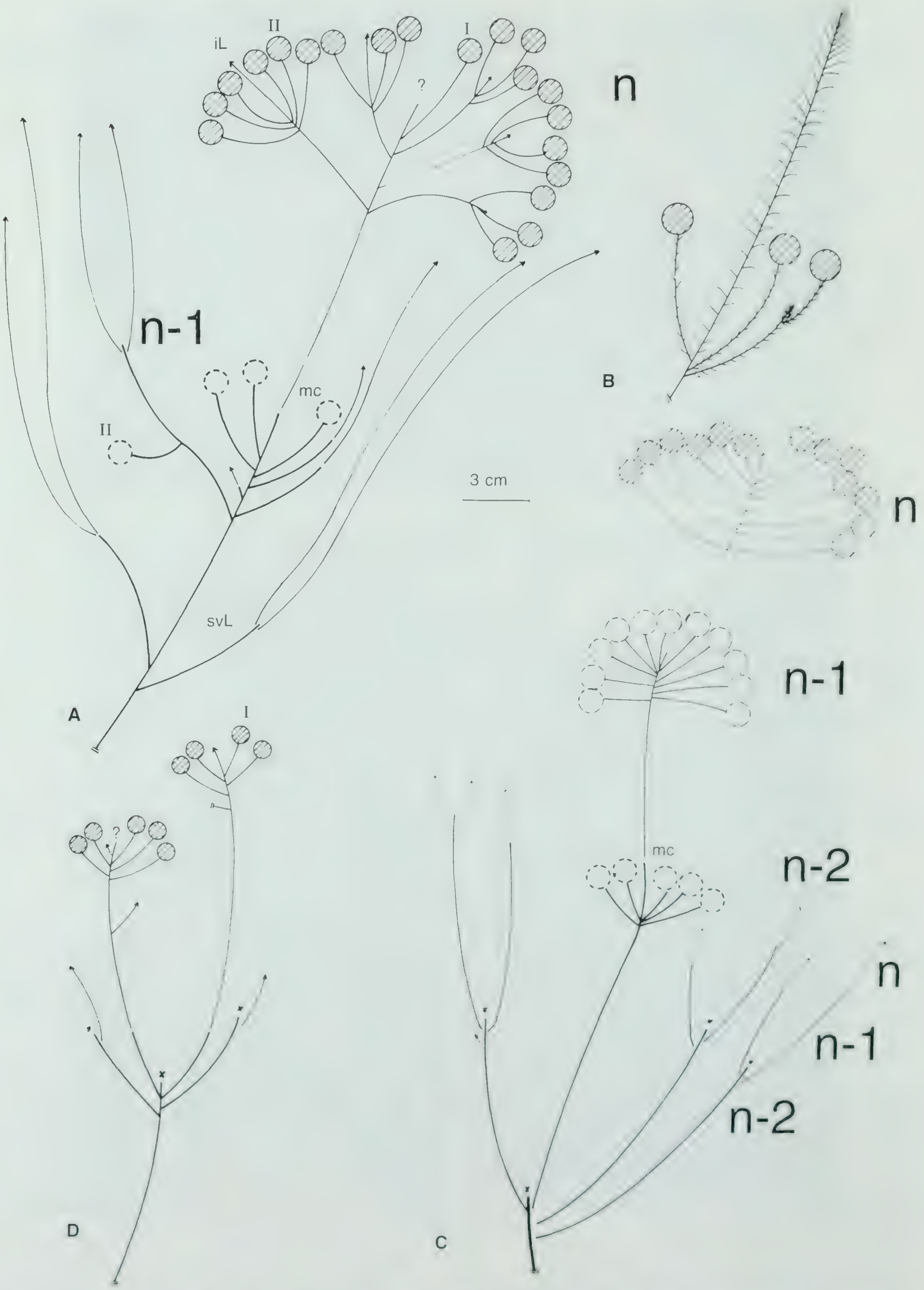


Figure 68 - **Brunia stokoei**. *A-D, profiles of flowering shoot systems. Note the monopodial connection of the SGUs and the diverse nature of the flowering zone, being simple in C and compound in A.*

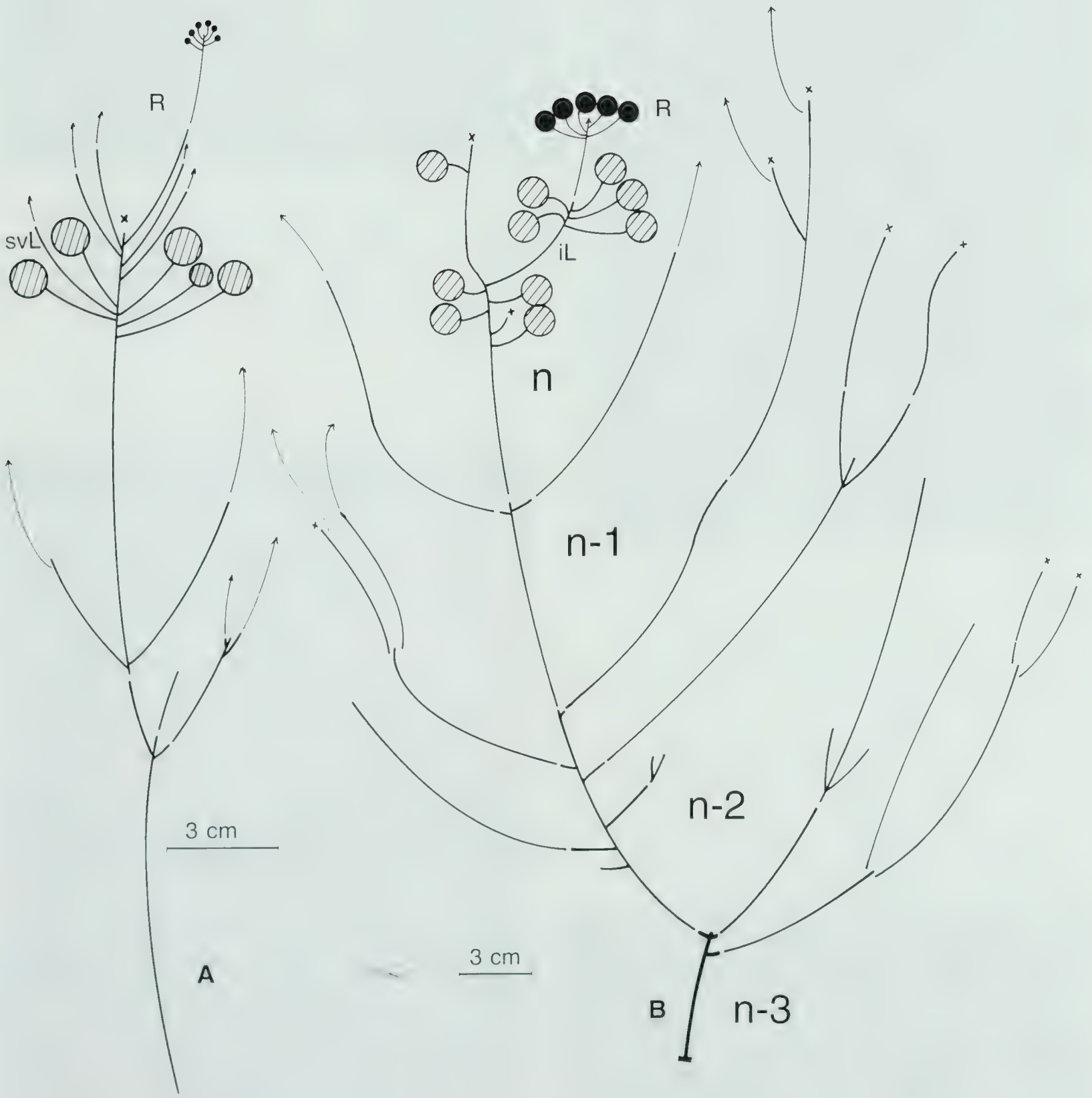


Figure 69 - **Brunia stokoei**. *A,B, profiles of shoot systems at an early (A, August 1996) and late postfloral stage (B, December 1996). Note the subterminal position of the renewal shoots above the flowering zone in A, and the continuation of the shoot system from a lateral flowering shoot in B (compare with fig. 67C).*

Figure 70 - **Brunia alopecuroides**. *Flowering shoot system of a shrub from Mount Lebanon. Note the deflorated inflorescences of the previous season at the base of figure A and the centrifugal age-gradient of the inflorescences of the present season in B.*

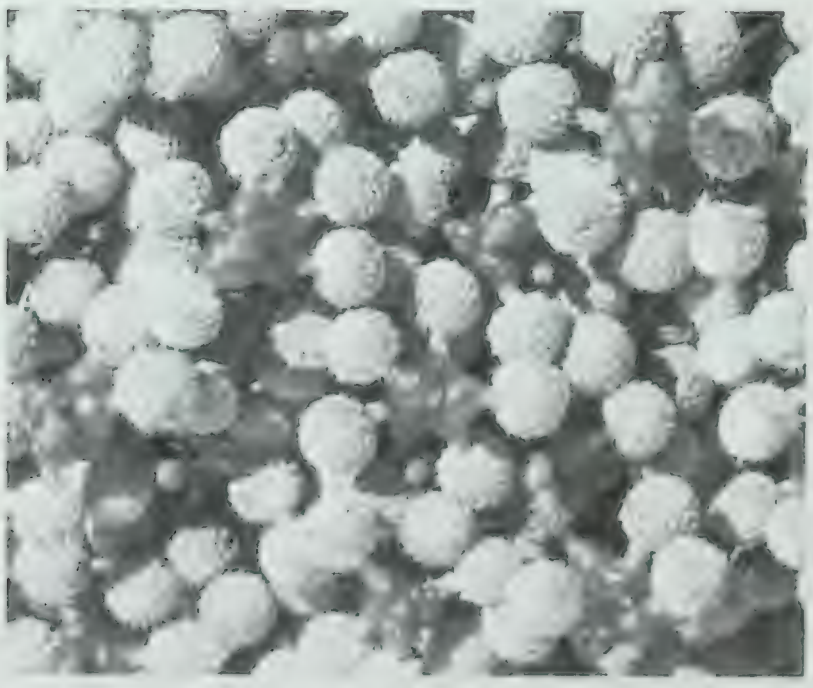


Figure 71 - **Brunia alopecuroides**. *Flowering shoot system of a shrub from Landrostkop (A) and two sympatric plants from Mount Lebanon (B,C). Note the analogous similarity between the brown shoot tips in A, the red swellings in B, and the infructescences in C*

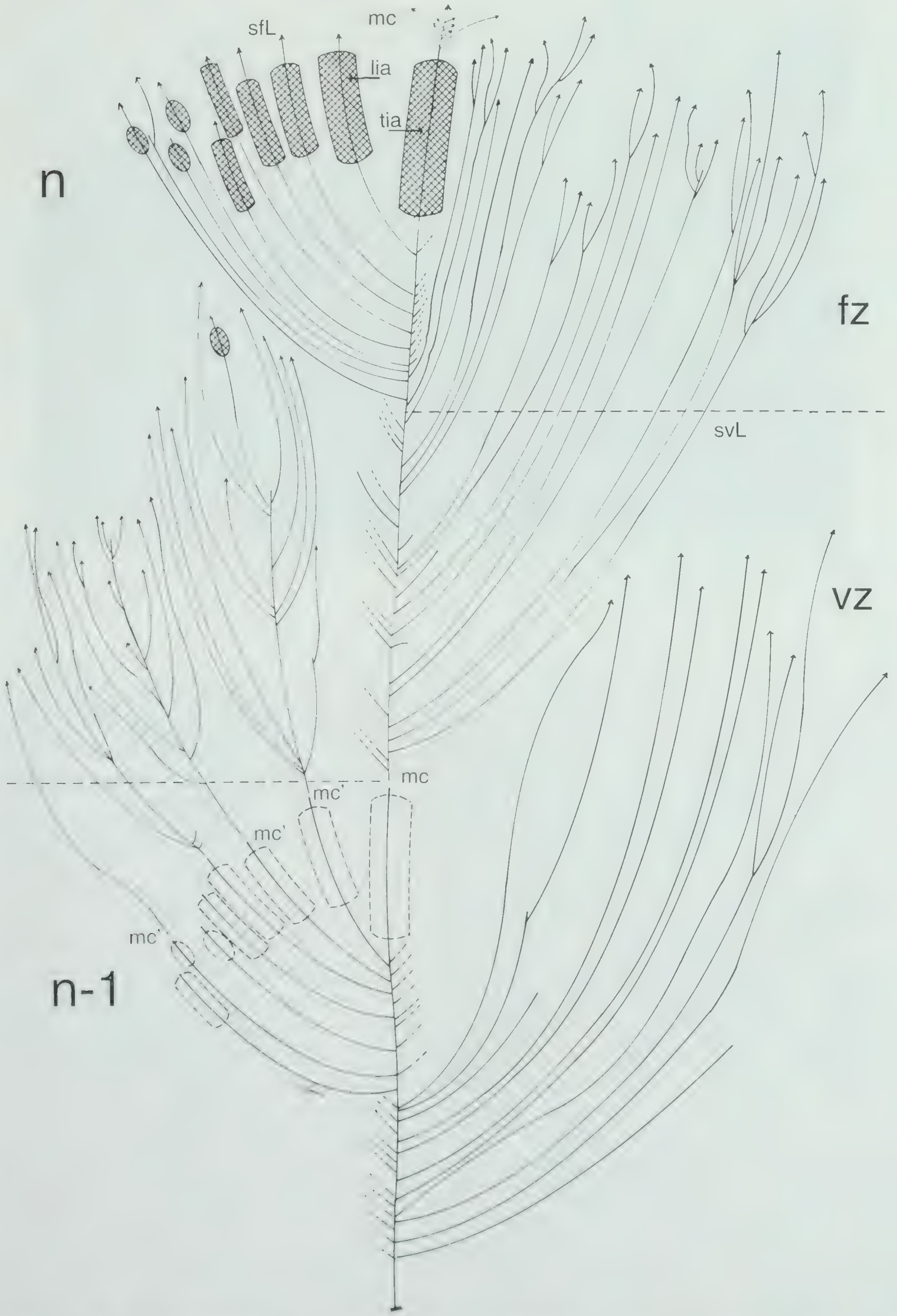
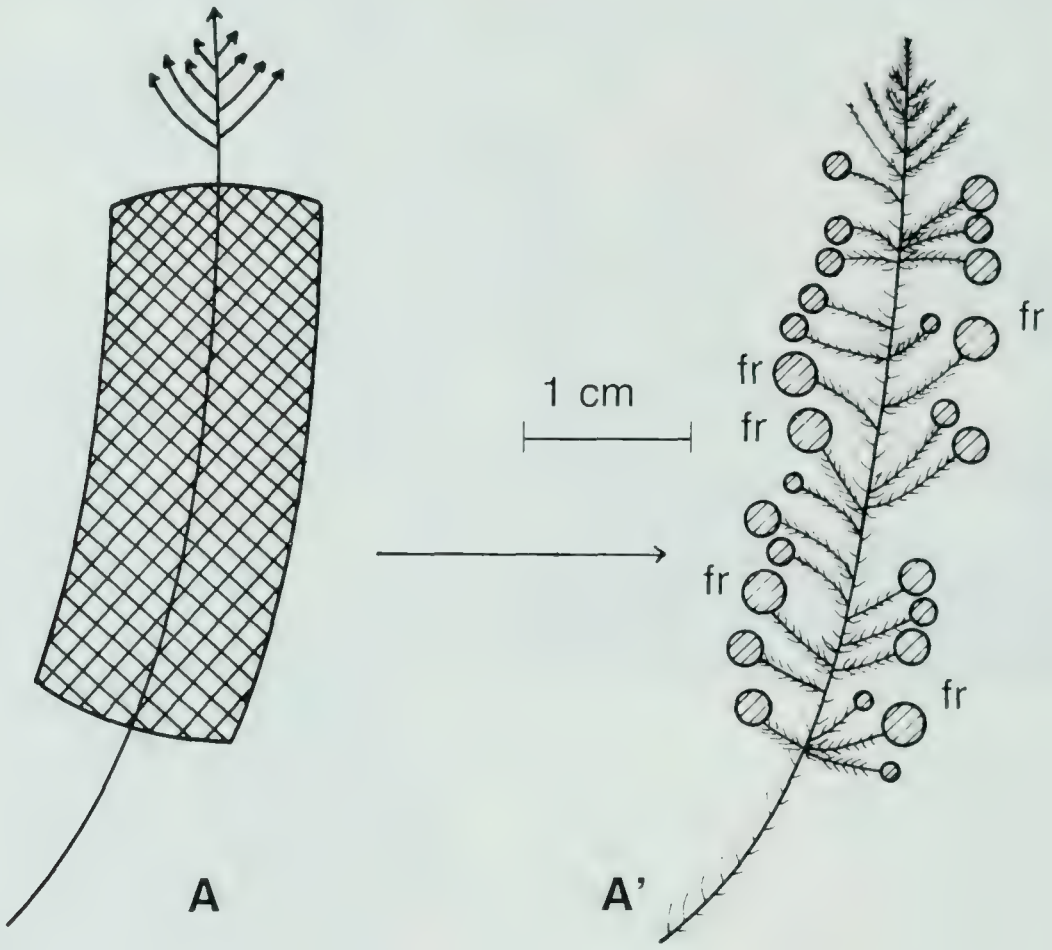


Figure 72 - **Brunia alopecuroides.** *Profile of a flowering shoot system, two seasons old, showing the monopodial connection of the SGUs concerned and the centrifugal decrease in inflorescence size (compare with fig. 73).*



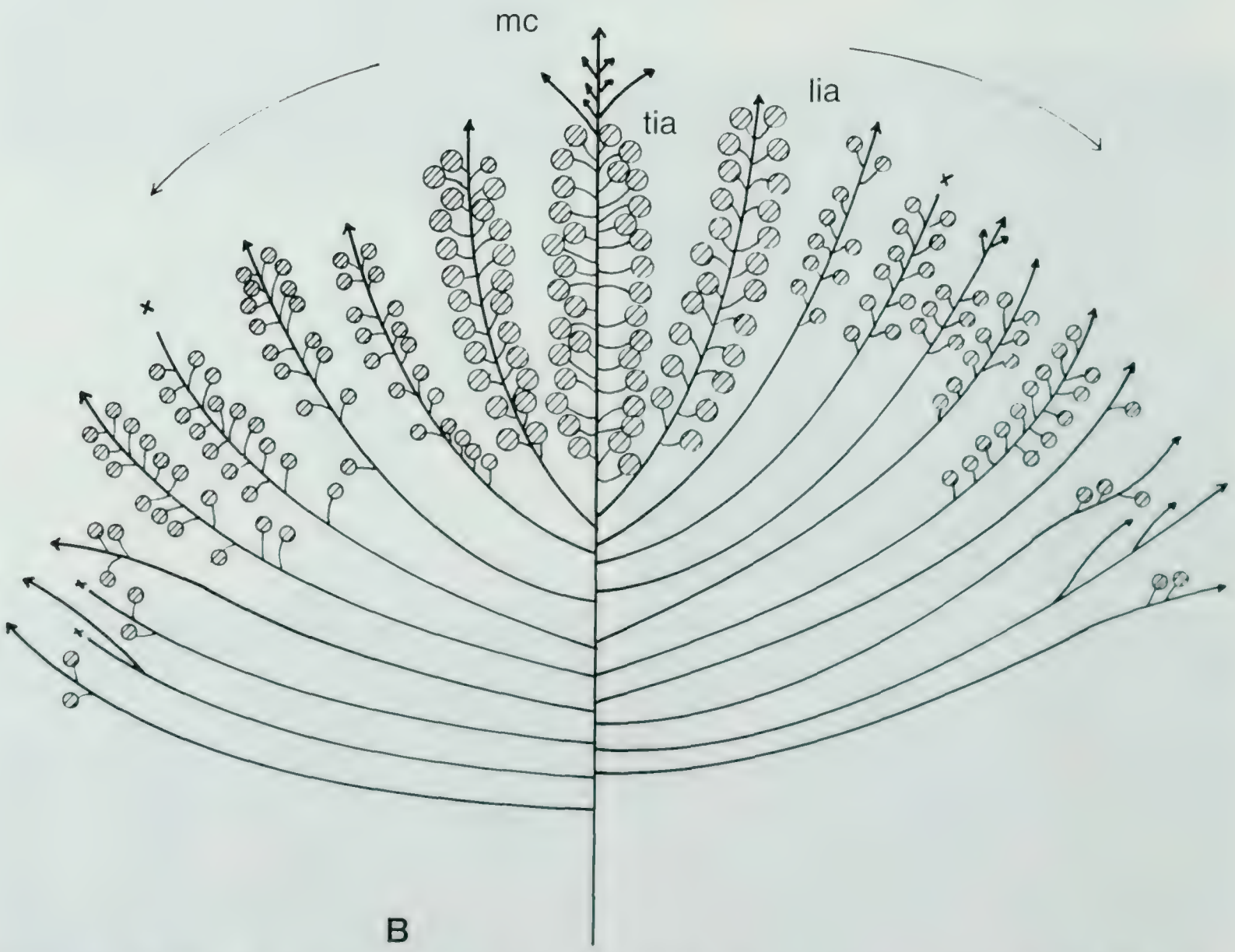


Figure 73 - **Brunia alopecuroides**. *Scheme (A) and profile (A') of a lateral aggregate of inflorescences showing the irregular arrangement and inequal size of the individual inflorescences. B, profile of a cluster of inflorescence aggregates showing the centrifugal flowering sequence (arrows) and the centrifugal decrease in number and size of inflorescences.* fr, *fruiting*

Figure 74 - **Brunia alopecuroides.** *Locality of a population within a restioid fynbos community at Landrostkop.*

Leaf metamorphosis and inflorescence structure. Like *Berzelia* the genus *Brunia* is characterized by the presence of pincushion-like inflorescences (fig. 75A,A′). However, with the exception of *B. alopecuroides*, all *Brunias* possess an involucre (fig. 75Ca-f: black). As with *Berzelia*, the stamens are exserted at anthesis. In *B. albiflora*, *B. stokoei* and *B. alopecuroides* these organs are of equal length, while in the other species four (*B. macrocephala*), three (*B. neglecta*) or two (*B. nodiflora*) stamens are longer than the remainder (Pillans 1947:178). Only the longer stamens, always oriented abaxially, are clearly exserted.

Dependent on the species, inflorescences may comprise 50 to 300 individual florets (fig. 75Ca-g:7) which are tightly packed on the receptacle. The ontogeny of the inflorescences could not been studied because of insufficient material, but some evidence suggests a determinate arrangement: (1) the flowering sequence may be centripetal (e.g. *B. nodiflora*) or divergent (e.g. *B. stokoei*, compare with Anonymus 1987:62), flowering often commences with a terminal floret. (2) in *B. nodiflora* the axillary flowers have a zygomorphic androecium, but the terminal flower has five stamens of equal length. (3) in *B. alopecuroides* the flowers are not as densely packed as in the remaining species and the terminal flower can be clearly seen. The inflorescences of at least four species are cephaloids and it is presumed that cephaloids are present in the remaining species also (fig. 75A,A′).

According to Pillans (1947:178) each floret is subtended by a bract, but only rarely by two prophylls (e.g. in *B. alopecuroides)*. In practice it is difficult to determine which and how many bracts are associated with a single floret. In *B. laevis* (fig. 75Cc) prophylls are entirely lacking, while in the remaining species additional bracts are present, either differing from those subtending the florets (fig. 75Cb,d-g) or resembling them closely (*B. nodiflora*, fig. 75Ca). In the latter case it is possible to interpret these structures as sterile bracts. In all species, except *B. alopecuroides*, the bracts, prophylls and sepals are densely covered with hairs, which presumably protect the young floral primordia. Protection is increased by the inward curvature of the subtending bracts and prophylls, which cover the young florets completely. This may also be the reason for the increased bract length (fig. 75C4,5).

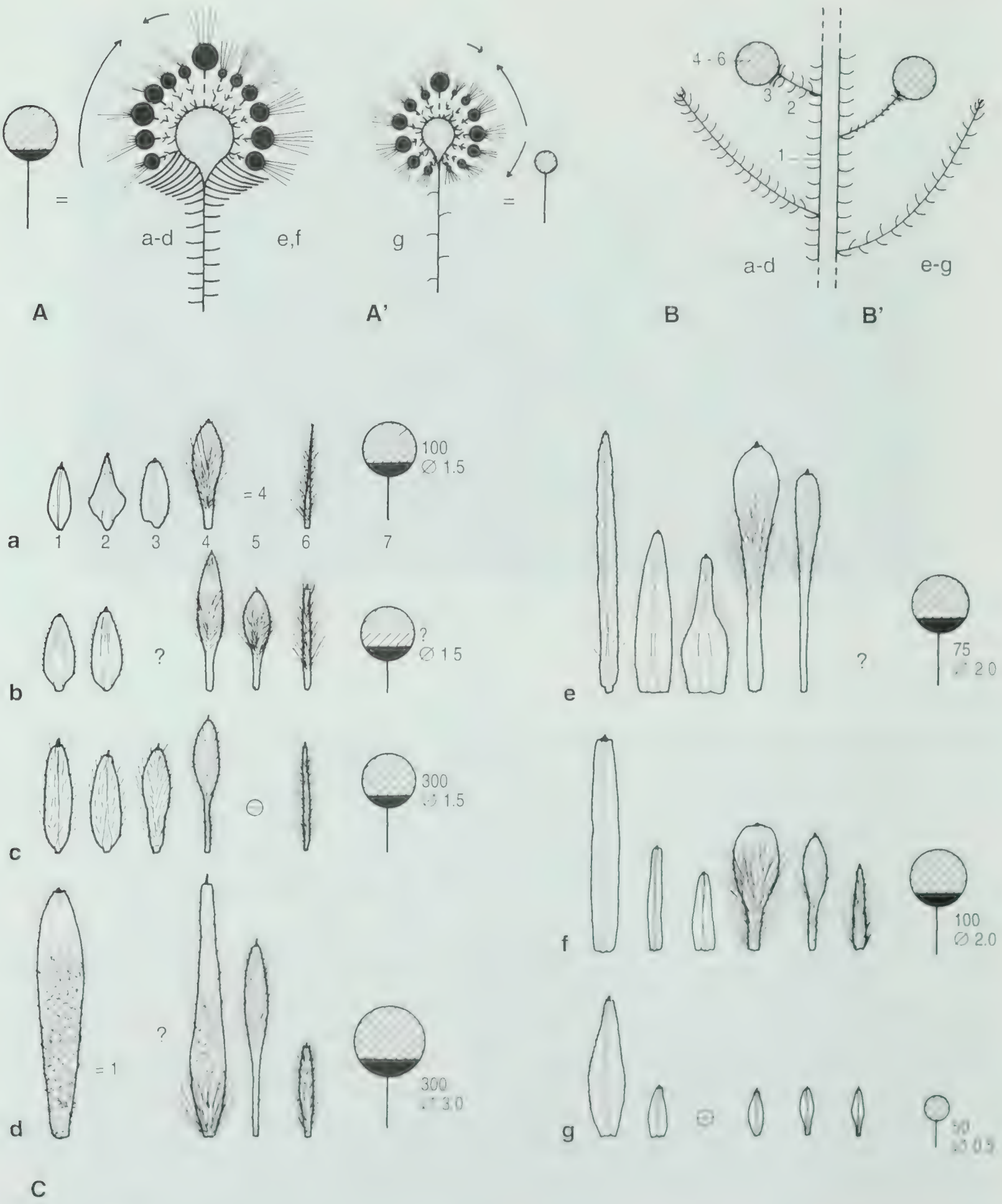


Figure 75 - **Brunia***: **Leaf metamorphosis and inflorescence structure**. A,A', profiles of inflorescences showing the pincushion-like habit, the terminal flower, the flower-subtending bracts and prophylls, the flowering sequence (arrows), the involucre which is missing in* B. alopecuroides *(A') and the symmetry of the androecium which is zygomorphic in some species (A: a-d), B,B', profiles of flowering shoots showing the different foliage of the lateral flowering short-shoots, C:1-6, leaf metamorphosis of the species analyzed, 1, foliage, 2, leaf or bract at the flowering short-shoot, 3, involucral bract, 4, flower-subtending bract, 5, prophyll, 6, sepal, C:7, shape and size of the individual inflorescences and their average number of florets, a,* B. nodiflora, *b,* B. neglecta, *c,* B. laevis, *d,* B. macrocephala, *e,* B. albiflora, *f,* B. stokoei,, *g,* B. alopecuroides.

the numbers 1-6 *in B correspond to the numbers* 1-6 *in C;*
the numbers in C'7 represent the average number of florets per inflorescence
and, below, the diameter of the inflorescences in cm,
?, presence of organ not assured.

Leaf metamorphosis may be either gradual (fig. 75B) or abrupt (fig. 75B′). In *B. nodiflora*, *B. neglecta*, *B. laevis* and *B. macrocephala*, the flowering short-shoots are covered with leaves (a-d), while in *B. albiflora*, *B. stokoei* and *B. alopecuroides* they are bracteate (e-g). As is illustrated in fig. 75B,B′ the nature of the foliage clearly indicates the separation of the individual inflorescences from each other.

B. alopecuroides merits special comment in that this species shares many characters with the genus *Berzelia:* the double-racemose arrangement of inflorescences, the obligate lack of a terminal inflorescence, the small size of individual inflorescence, the lack of an involucre (fig. 75Cg:7), the equal length of the five stamens, the glabrous bracts and the abrupt leaf metamorphosis. Besides these characters, *B. alopecuroides* occasionally also produces red "cushions" at the base of the peduncles.

In fig. 71B,C the flowering zones are shown of two shrubs which grow sympatrically at Mount Lebanon. From a distance both are characterized by cream-coloured inflorescences and by conspicuous red structures which are however analogous to each other. The one plant (B), at early anthesis, shows the conspicuous red swellings which are known only from some *Berzelia* species (compare with p. 66). The other plant (C) is at full anthesis. According to the basipetalous flowering sequence, the central inflorescences are already in fruit while the remainder are still flowering. When fruiting the sepals of the individual flowers start to swell and turn red. Thus each of the infructescences assumes a conspicuous red, berry-like appearance which contrasts with the star-like appearance of the cream-coloured petal tips and anthers (fig. 70B). It is not known whether birds are attracted by the `berries´ or not and, thus, the biological function of the red swellings which may mimic ripe fruits is open for discussion. In this context the brown shoot tips of a third plant from Landrostkop (fig. 71A) are remarkable in showing a similar spot-like pattern as do the red cushions (fig. 71B) and the red infructescences (fig. 71C).

Summary: Figure 76 gives a general summary of the branching and flowering patterns of the genus *Brunia*. In fig. 76A the reference system (RS) is shown. It is subdivided into an apical zone (az) bearing a terminal determinate inflorescence, a renewal zone (rz) below this inflorescence and an extended branching zone (bz) which is further subdivided into a distal flowering zone (fz), a transitional zone (tz) and a proximal vegetative zone (vz). The individual inflorescences are cephaloids, each with a terminal flower (tf). They are arranged at the end of unbranched short-shoots or at branched determinate (dL) or, more rarely, indeterminate lateral shoots (iL) ranging from branches of the 1st (I) up to 3rd (III) order. The flowering zone is organized in a conjunct way, but occasionally exhibits most extensive branching in the central region (mesotony). It is interspersed with sylleptic vegetative shoots (svL) arising from the main axis up to the branches of 3rd order.

Fig. 76B-H illustrate the variability of the RS:

- The terminal inflorescence may be lacking. In this instance, the apex of the dominant shoot is able to grow on in the next season, giving rise to monopodial connection of the SGUs concerned (B: mc). The sympodial units of e.g. *B. albiflora* may age up to five seasons in this manner.
- The renewal zone may be lacking and compensated for in various ways by vegetative shoots arising from the flowering zone or from the vegetative zone below (C). In *B. albiflora* an example is shown where the renewal zone of a lateral flowering shoot of 1st order of branches undertakes the function of renewal. In *B. stokoei* all renewal shoots may be lacking within a flowering SGU, resulting in a strictly reproductive shoot system.
- The time of renewal is variable: in *B. nodiflora* the shoot system of the next season is already growing out when the inflorescences of the present season are still at anthesis (D).
- The flowering zone varies in the number of lateral shoots, the number of inflorescences and the number of the order of branches (E). In *B. macrocephala* it is often completely lacking.
- The flowering zone may be homogenized and disjunct (F) as is clearly demonstrated by *B alopecuroides*.
- The flowering lateral shoots may be indeterminate (G) and able to continue their growth in the next season
- Vegetative shoots within the flowering zone may be lacking and the entire vegetative zone may remain unbranched (H) In the extreme case no vegetative renewal shoots are present in a SGU and the flowering shoot system concerned dies off completely.

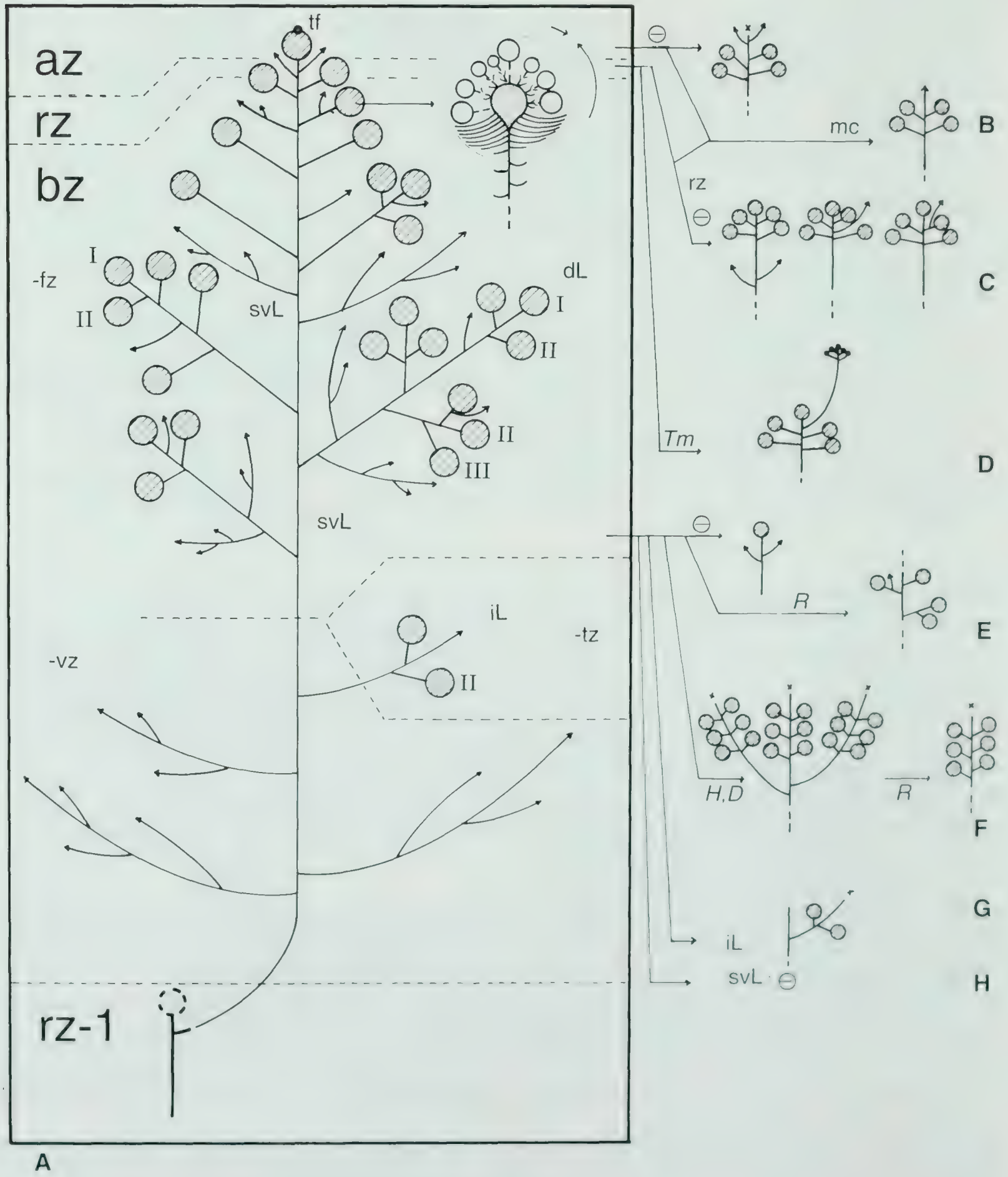


*Figure 76 - **Model of the genus* Brunia. *A, the reference system (RS) of the genus showing the terminal cephaloid, the renewal zone below and the much branched flowering and vegetative parts of the branching zone. B-H, variation of the RS concerning the absence of the terminal inflorescence and the growing activity of the apex (B), the position of renewal shoots (C), the precurrent development of the next season's shoots (D), the quantitative equipment of the flowering zone (E), the arrangement of the inflorescences (F), the presence of indeterminate flowering shoots (G) and the absence of sylleptic vegetative shoots (H)*

D, disjunction, R, reduction, Tm, shifting in time, tz, transitional zone

A comparison between the reference systems of the genera *Berzelia* (fig. 50) and *Brunia* (fig. 76) shows (1) that the RS of *Brunia* is characterised by a terminal inflorescence which is strictly absent in *Berzelia*. (2) the flowering zone in *Brunia* is conjunct and interspersed with vegetative shoots, while the flowering zone in *Berzelia* is disjunct and more clearly separated from the vegetative part of the branching zone. (3) the sylleptic flowering lateral shoots in *Brunia* are able to bear vegetative shoots while they are strictly reproductive in *Berzelia*. These differences, as well as the different size of the individual inflorescences, the presence or absence of an involucre and the symmetry of the andreocium express only different tendencies in the two genera. As all these characters are highly variable, the branching and flowering patterns of *Brunia* and *Berzelia* do not offer a single character which clearly distinguishes the species of the two genera as presently delimited.

3.4 *Linconia* L.

Linconia *is a small genus with three rare species, all of which occur in the mountain fynbos of the SW Cape. Only a few herbarium specimens of* L. cuspidata *and* L. alopecuroides *were available for the present study. Thus, the analysis remains fragmentary.*

Growth and branching pattern. *L. alopecuroides* and *L. cuspidata* are small heath-like shrubs with dense foliage and (sub)terminal inflorescences. Their habit is strikingly diverse. *L. alopecuroides* reaches 60 cm in height (Pillans 1947:131) and has large, spike-like flower clusters (fig. 77A), whereas *L. cuspidata* is much smaller, with shrubs no more than 30cm in height (Pillans 1947:132), much-branched and characterized by small, spherical inflorescences (fig. 77B,C). *L. alopecuroides* occurs in dense fynbos vegetation while *L. cuspidata* is a rock-crevice species.

Cursory examination of a flowering shoot of *L. cuspidata* (fig. 77C) suggests a sylleptically branched shoot system which flowers simultaneously at the end of the main axis and several lateral branches. This first impression is deceptive. A closer examination reveals the presence of alternating zones of spreading and more appressed leaves (fig. 78C,D). The latter are smaller and more densely arranged than the former and have distinctly curled hairs on their basal parts (fig. 80A: 1-5). Internodes of different length are also seen on older parts of the shoot system (fig. 77D: di,wi) where the leaf-blades have already been shed leaving the persistent leaf-bases behind (fig. 80B-B´). Flowers may arise in either zone, i.e. both spreading and appressed leaves may function as flower-subtending bracts.

The alternating zones of foliage and internodes of different length are interpreted as being the external symptoms of the growth rhythm of the plant. It is suggested that each of the SGUs has a proximal zone bearing spread leaves and a distal zone bearing appressed leaves, the latter indicating the end of the season concerned (fig. 78D´, 80C). The long leading shoots which flower terminally and bear several such alternating zones of foliage therefore represent several monopodially connected SGUs with persistent leaves (fig. 78A-D´). As far as possible the supposed seasons are indicated by a line in fig. 78C,D. A monopodial connection of five or more SGUs of different length appears quite common. As fig. 78B: n and fig. 78D´ show the individual SGU does not necessarily flower but can also remain in the vegetative state. On the other hand it is possible for lateral shoots to grow out sylleptically and flower simultaneously with the main axis (fig. 78B: sfL). As in the case of the leading shoot, they are able to continue their growth in the next season.

If this interpretation is correct the analogy between a perennial long shoot and an individual SGU is the result of (1) several monopodial inserts, (2) short SGUs, (3) poor branching, (4) dominance of the main axis, (5) disappearance of faded flowers and fruits without leaving a trace and (6) persistent leaves.

L. alopecuroides is not characterized by a comparable alternate foliation. But there are also zones with dense internodes which may indicate the end of the seasons concerned (fig. 79A,B,D: di). It has been assumed that the zone of dense internodes corresponds to the position of the former inflorescence which is shed without leaving any traces (fig. 79D: di, rz). Accordingly, the individual SGU is much longer than in *L. cuspidata*. The inflorescences again are subterminally arranged. A tuft of sterile leaves is always present, thus, the possibility for a monopodial shoot connection is principally given. Sylleptic lateral shoots occur quite often and apparently flower together with the main inflorescence which always has the highest amount of flowers (fig. 79B). When the apex dies off renewal shoots are formed above the inflorescence (fig. 79D,E: R). They seem to develop very late as no primordia of prospective renewal shoots have been found in the specimens analysed.

Figure 77 - **Linconia**. *Flowering shoot systems of* L. alopecuroides *(A; Wurts 402, NBG) and* L. cuspidata *(B; Stokoe s.n., NBG, C, D, Schlechter 9273, B).*

di, *dense internodes,* wi, *wide internodes; compare B,C with fig. 78 C,D.*

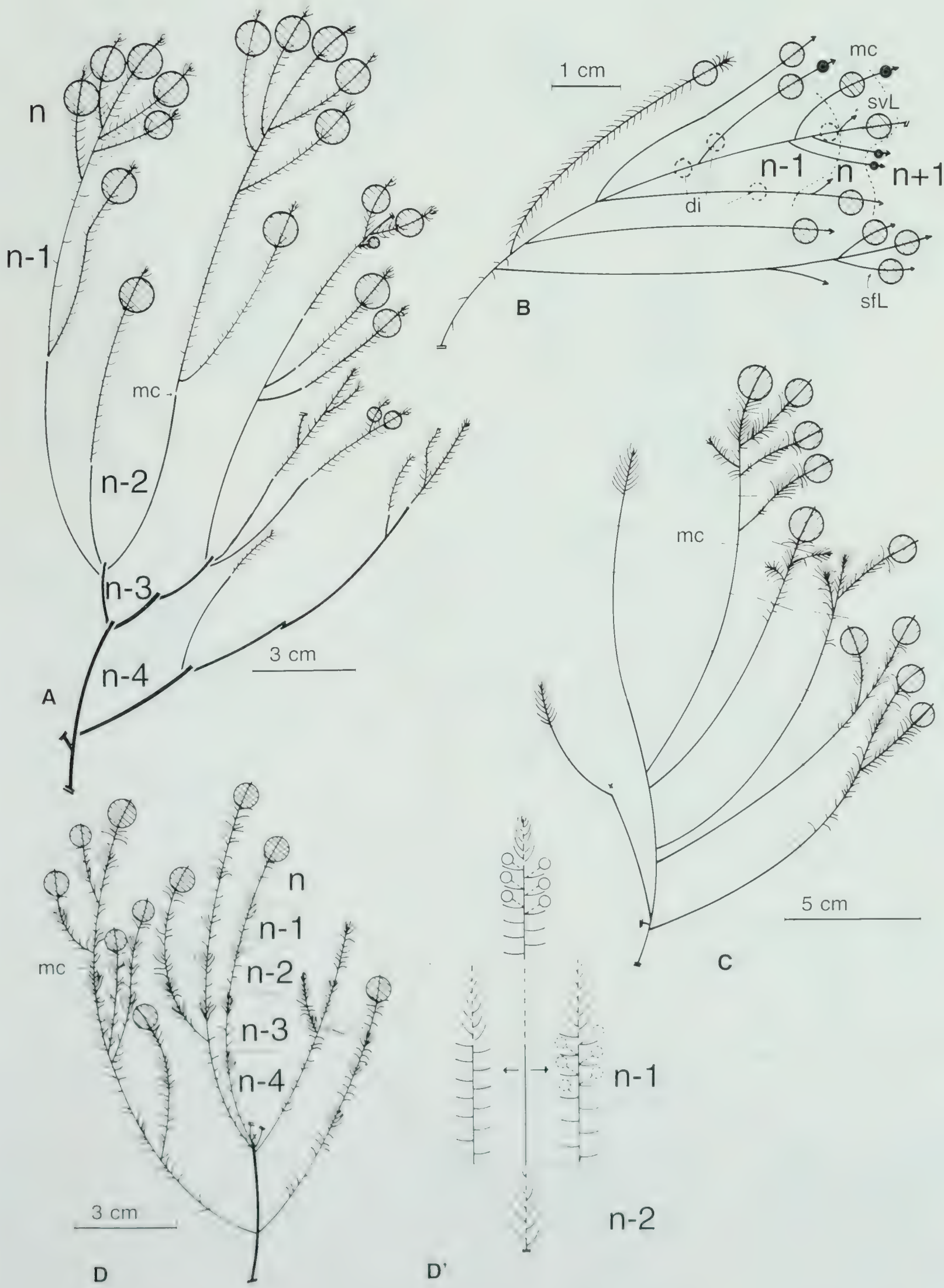


Figure 78 - **Linconia cuspidata**. *Profiles of flowering shoot systems.*
di, dense internodes; compare C,D with fig. 77B,C.

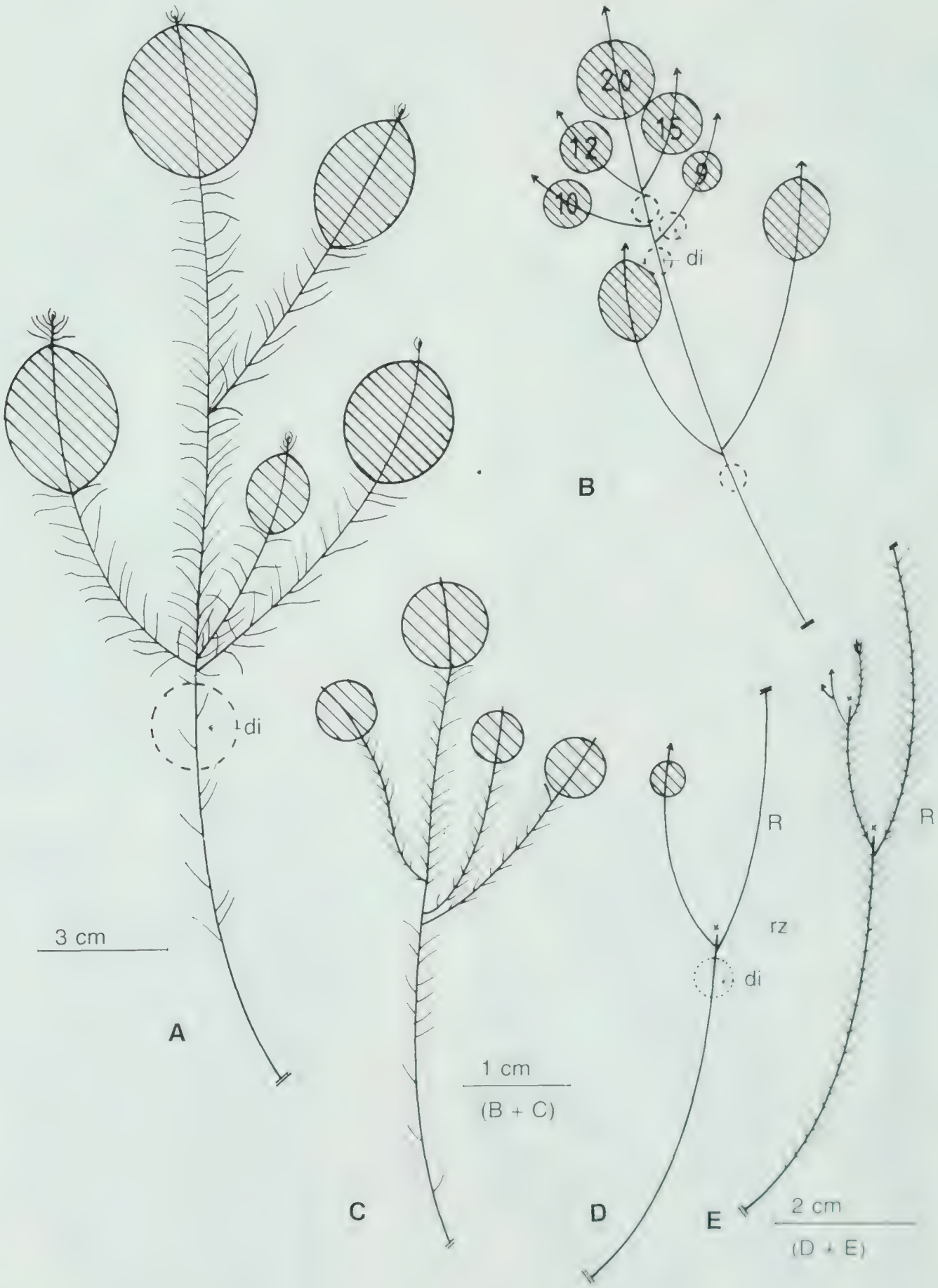
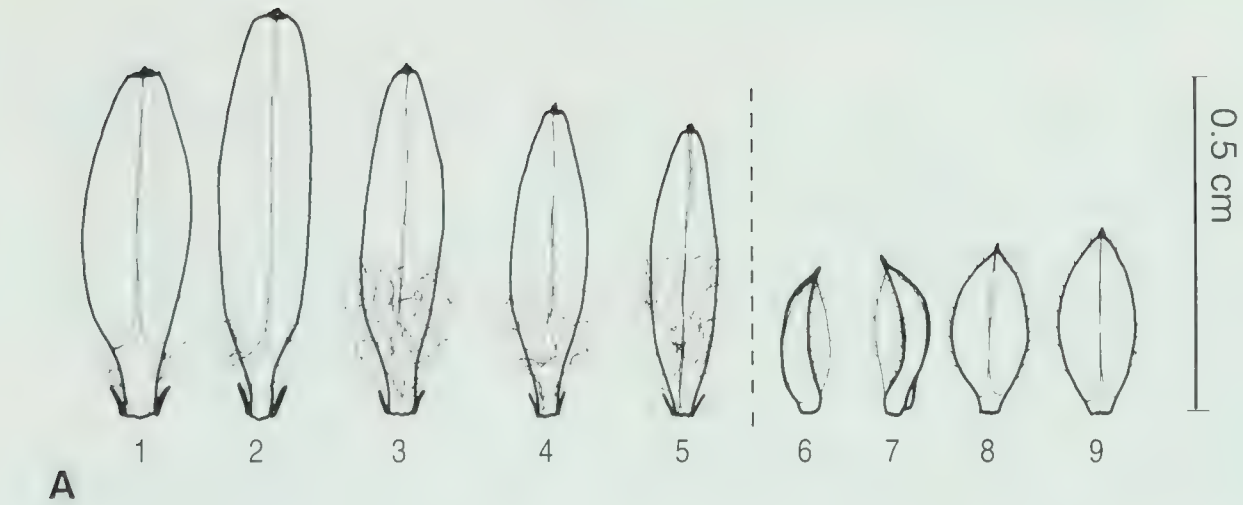
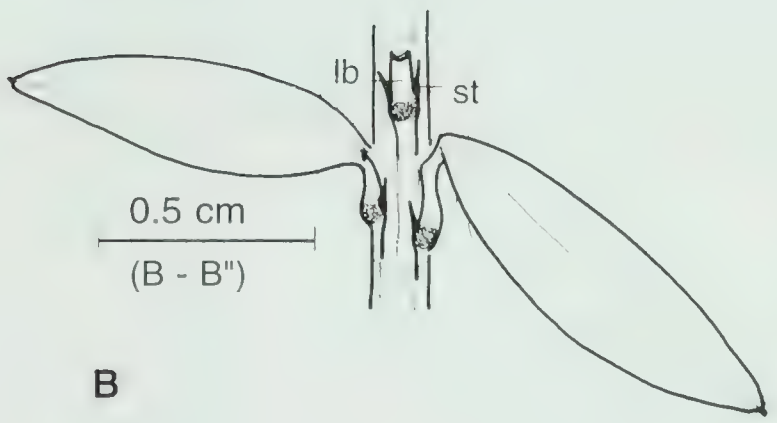
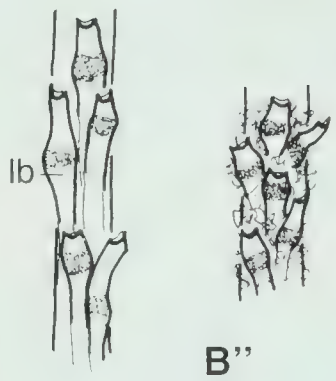


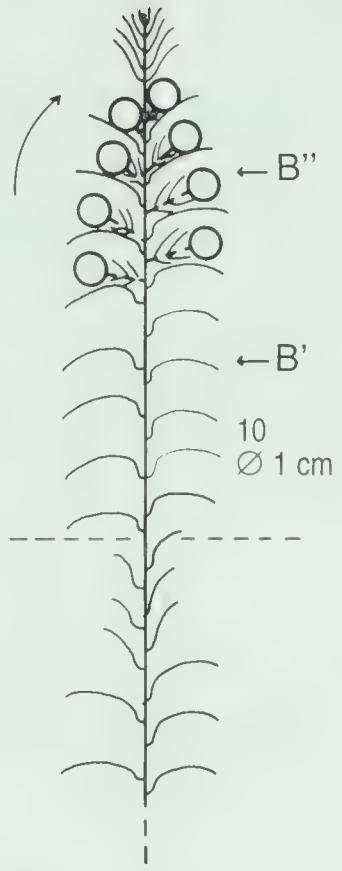
Figure 79 - **Linconia alopecuroides**. *Profiles of flowering shoot systems.* di, *dense internodes; the numbers in* B *correspond to the number of flowers in the inflorescence concerned.*

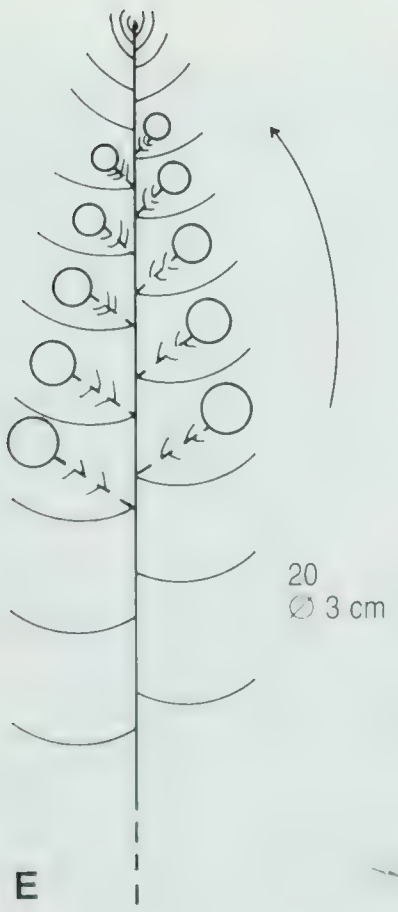
Leaf metamorphosis and inflorescence structure. Referred to each of the SGUs, the inflorescences of the genus *Linconia* are terminally arranged, or rather subterminally considering the tuft of leaves at the apex (fig. 80C,E). Each inflorescence has about 10 (*L. cuspidata*) or 20 (*L. alopecuroides*) flowers which are all laterally arranged and show an acropetal flowering sequence (fig. 80C,E arrow). Each flower is subtended by a folious leaf and is surrounded by four thin bracts (fig. 80D). In *L. alopecuroides* the subtending leaves differ from the sterile leaves only in being smaller (fig. 80F 1-3), whereas in *L. cuspidata* they additionally are covered with curly hairs (fig. 80A 1-5). An abrupt change within the leaf metamorphosis is seen in both species between the subtending leaves and the flower-surrounding bracts which are clearly distinct from each other in size, shape and condition (fig. 80A: 6-9, F: 4-7).

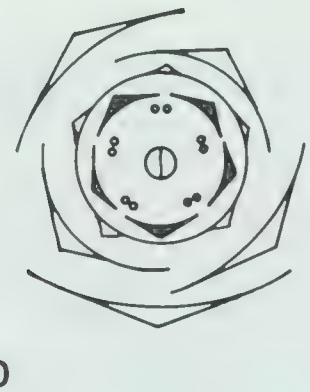












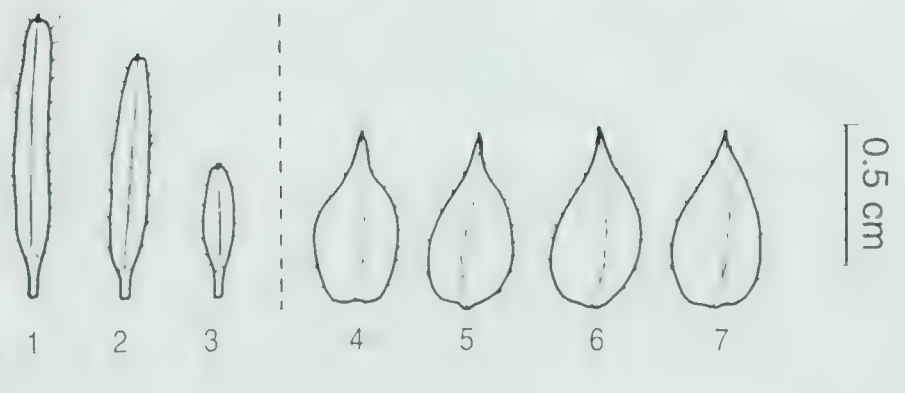


Figure 80 - ***Leaf metamorphosis and inflorescence structure in the genus*** **Linconia**. *A-D*, L. cuspidata*: A, leaf metamorphosis, 1,2, relatively large, sparsely tomentose leaves of the zone with wide internodes, 3-5, smaller leaves with curly hairs at the base of the zone with dense internodes, 6-9, bracts round each of the flowers; B-B'', details of different parts of the stem: B,B', zone with wide internodes and spread leaves, in B' only the persistent leaf bases present, B'', zone with dense internodes, only the persistent leaf bases present which are like the stem densely covered with hairs; C, profile of an individual seasonal growth unit with a terminal inflorescence: the flowers are arranged laterally and are surrounded by four bracts each, the apex continues its growth; D, diagram of a lateral short-shoot with the subtending leaf, four bracts and the terminal flower; E,F,* L. alopecuroides*: E, profile of an inflorescence, F, leaf metamorophosis: sterile folious leaf (1), proximal (2) and distal (3) flower-subtending leaf, bracts (4-7).*

lb, *leaf base,* st, *stipule;*

the numbers in C and E correspond to the average number of flowers per inflorescence and the average diameter of the inflorescence; arrows in C,E: flowering sequence.

Summary. The model of the genus *Linconia* in fig. 81 is the result of the interpretation illustrated above. The apex continues to grow for several seasons connecting the individual SGUs in a monopodial way (B: mc). Yet, for the reason of comparison, the RS shows a one season old, flowering sympodial unit (A).

The apex always remains open, that is a terminal flower never appears. The renewal zone (rz) is above the inflorescence. Besides the flowering short-shoots the branching zone (bz) has no further branches or at least not more than a few vegetative or flowering lateral shoots (C: svL, sfL) The inflorescence looks like a spike or a head, but is characterised by a high amount of bracts around each flower.

Altogether the branching pattern and inflorescence structure of *Linconia* are very similar to those of *Audouinia capitata*. The similarities are reflected in the models of the two genera. Especially remarkable is the similarity in the organisation of the inflorescences and the leaf metamorphosis which shows exactly the same abrupt change between the flower subtending leaf and the bracts around each flower. The repetitive inserts of monopodial units within a sympodial unit is an additional shared character but as this is quite frequent within the Bruniaceae it is a less specific one.

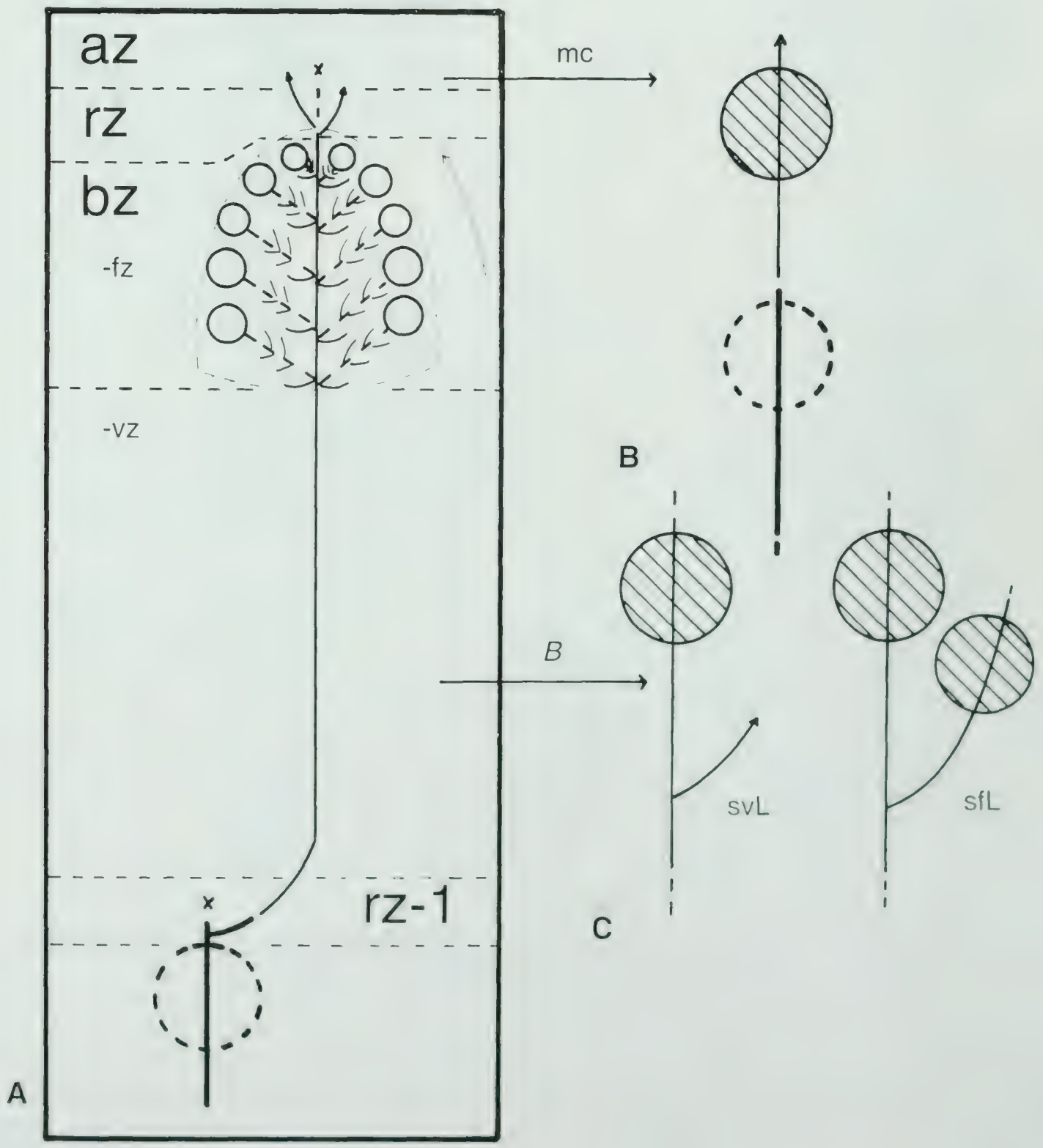


*Figure 81 - **Model of the genus* **Linconia**. *A, the reference system (RS) of the genus: the branching zone is not branched below the inflorescence, the inflorescence is a cluster of lateral short-shoots, the renewal zone is above the inflorescence, the apex remains open. B,C, variations of the model: B, monopodial connection of seasonal growth units, C, sylleptic branching within the branching zone.* *B, branching*

3.5 *Lonchostoma* Wikstr.

The genus has five species. L. esterhuyseniae *is known from only one locality near Swellendam. The other four species are distributed from Caledon to Clanwilliam/Ceres (Strid 1968).*

L. monogynum *has been found at the Kogelberg Nature Reserve (fig. 2C),* L. pentandrum *is cultivated in the nursery of the Botanic Garden Kirstenbosch. In August 1996 it was in full flower (fig. 82A,B), end of November 1996 the inflorescences were deflorated and the renewal shoots were growing on (fig. 82C).* L. myrtoides, L. purpureum *and* L. esterhuyseniae *have been analysed from herbarium material.*

Lonchostoma *is said to have a sympetalous corolla and therefore occupies an isolated position within the Bruniaceae (Pillans 1947, Takhtajan 1987, Dahlgren & Van Wyk 1988). But Leinfellner (1964a) has shown that the corolla of* Lonchostoma *is not sympetalous at all: in fact the petals are postgenitally fused with the filaments resulting in a pseudosympetalous corolla..*

Growth and branching pattern. The shrubs are relatively low ranging from only 40 cm to 90 cm in height (Pillans 1947:134; Strid 1968:312). Their habit is characterized by a regular sympodially branching pattern, by more or less appressed leaves and by terminal flower clusters (fig. 83A-D).

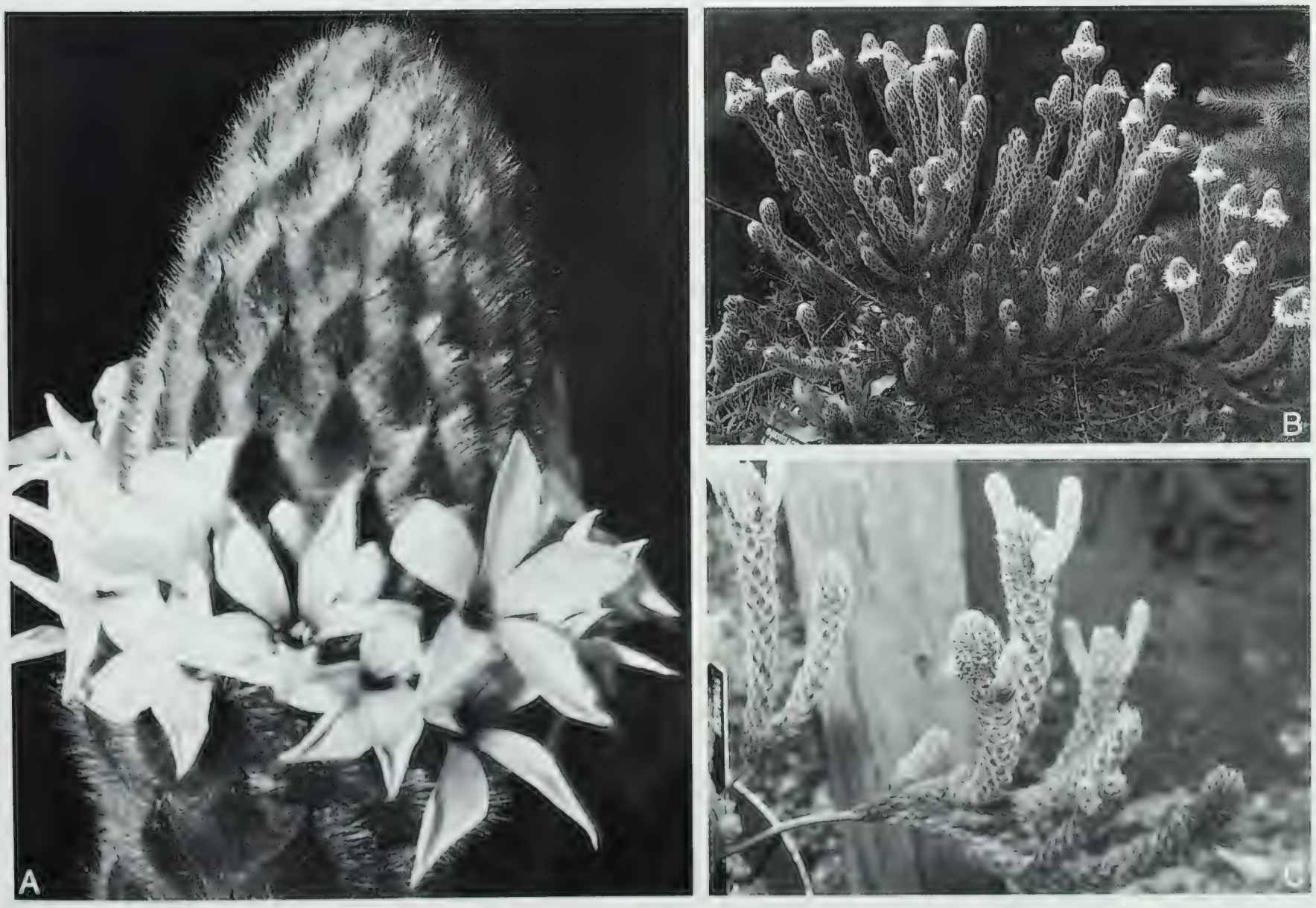


Figure 82 - **Lonchostoma pentandrum.** *A, inflorescence at the start of flowering, B, C, a plant cultivated at the nursery of the National Botanic Garden Kirstenbosch at the start of anthesis showing the acropetal flowering sequence (B) and after anthesis with renewal shoots below the terminal inflorescence (C).*

L. myrtoides (fig. 83A, 84A,A′) and *L. pentandrum* (fig. 82, 83B, 84B-B′′) follow the general scheme of a dichasial branching pattern with acrotonic renewal shoots. Below each of the terminal inflorescences two (rarely up to five) primordia are present which grow out and flower in the next season (cataleptic behaviour). The first leaves of the new shoots are clearly smaller than the following ones (fig. 89F). The leaves persist for about two to three seasons. In the first year they are densely hirsute, later they become glabrous and hard Because of the changing quality of the leaf surfaces with age it is possible to reconstruct the age of the individual parts of the shoot system. This is necessary as the general scheme varies in time:

- Occasionally one or more renewal shoots grow out earlier, that is in the same season as their mother axis (sylleptic behaviour). They remain either in a vegetative condition and flower in the next season (fig. 84A′,B′-B′′: svR/cfR) or flower concurrently with their mother axis (fig. 84A,B: sfR). In this case overtopping may result in an asymmetrical branching pattern.
- Occasionally a lateral shoot grows out one or more seasons later than the renewal shoots (fig. 84A′: lL). These shoots often die off after one season and may indicate a senescent state.

L. monogynum shows two different branching patterns. It is not clear whether they represent two different age stages or the difference between two populations:

- The first form is shown in fig. 83C and fig. 85A,B. The sympodial pattern is very clear, but because more than two lateral shoots generally grow out and flower, a pleiochasial instead of a dichasial pattern results. The lateral shoots are vigorous (+) or weak (-) flowering shoots or they remain vegetative (svL) and do not flower before the next season (cfL).
- The second form (fig. 85C-E) is characterized by sylleptic lateral shoots. The basal and medial ones (sfL) always flower together with the terminal inflorescence of the main axis (ti) while the apical ones either flower (fig. 85C) or remain vegetative (fig. 85E: svL, cfL).

L. purpureum (fig. 83D, 86) and *L. esterhuyseniae* (fig. 87) are smaller than the other species in respect of the size of the flowers and inflorescences and the length of the SGUs. Because of the small size an reconstruction of the branching pattern over several years is easiliy possible:

Fig. 83D and fig. 86A show a six season old shoot system of *L. purpureum*. Here too the different leaf surfaces permit recognition of the different age stages. In general four cataleptic lateral shoots occur in each season: two vigorous shoots (+), which flower and renew the shoot system (cfR), one flowering shoot (-) which remains markedly shorter than the two renewal shoots (cfL) and one vegetative shoot (cvL) which does not flower before the next season, if at all. The different length of the cataleptic shoots results in a branching pattern which is more or less determined by the two leading shoots (+) of each season. However, at the periphery of the shoot system the cataleptic shoots are similar in length as is seen in fig. 86A. Indeed, the number of the lateral shoots of the 5th order varies, dependent on the quality of the shoots of the 4th order of branching, but the length of the shoots growing out is more or less equal.

L. esterhuyseniae has a habit similar to that of *L. purpureum*. Nevertheless this species is completely different from the other *Lonchostoma* species. As it is seen in fig. 87 the apex occasionally continues to grow on (mc), that is the apex does not always die off after having formed the inflorescence but may flower a second time As is characteristic for the lateral shoots, the first leaves of the reactivated main axis are smaller than the following ones, thus indicating a new seasonal growth impulse.

Leaf metamorphosis and inflorescence structure. The inflorescences are arranged terminally About 20 flowers (less in *L. esterhuyseniae*, fig. 87A) are crowded together forming a spherical or cylindrical cluster (fig. 83, 88). Each flower is subtended by a folious leaf and two (to three) bracteate prophylls (fig 89A-E) The open apex of the inflorescence is clearly visible (fig. 88) and except in *L. esterhuyseniae* always dies off after having produced the flowers. The inflorescences are by no means separated from the vegetative part of the shoot Below them the primordia of the renewal shoots (rz) are present, a fact which may cause the retarded anthesis of the distal flowers (fig 88B arrows) Apart from that the flowering sequence is acropetal (fig 88A,C′,C′′ arrows) After anthesis the flowers and fruits fall off solitarily leaving a hairy inflorescence axis behind (fig. 83B, 84 A,B: I), which likewise falls off with time.

Figure 83 - **Lonchostoma**. *Flowering shoot systems of* L. myrtoides *(A; Compton 16225, BOL),* L. pentandrum *(B; Compton 18801, NBG),* L. monogynum *(C. Esterhuysen 15789, BOL), and* L. purpureum *(D; Goldblatt 1646, NBG).* I, *inflorescence axis, compare D with fig. 86, and C with fig. 85A.*

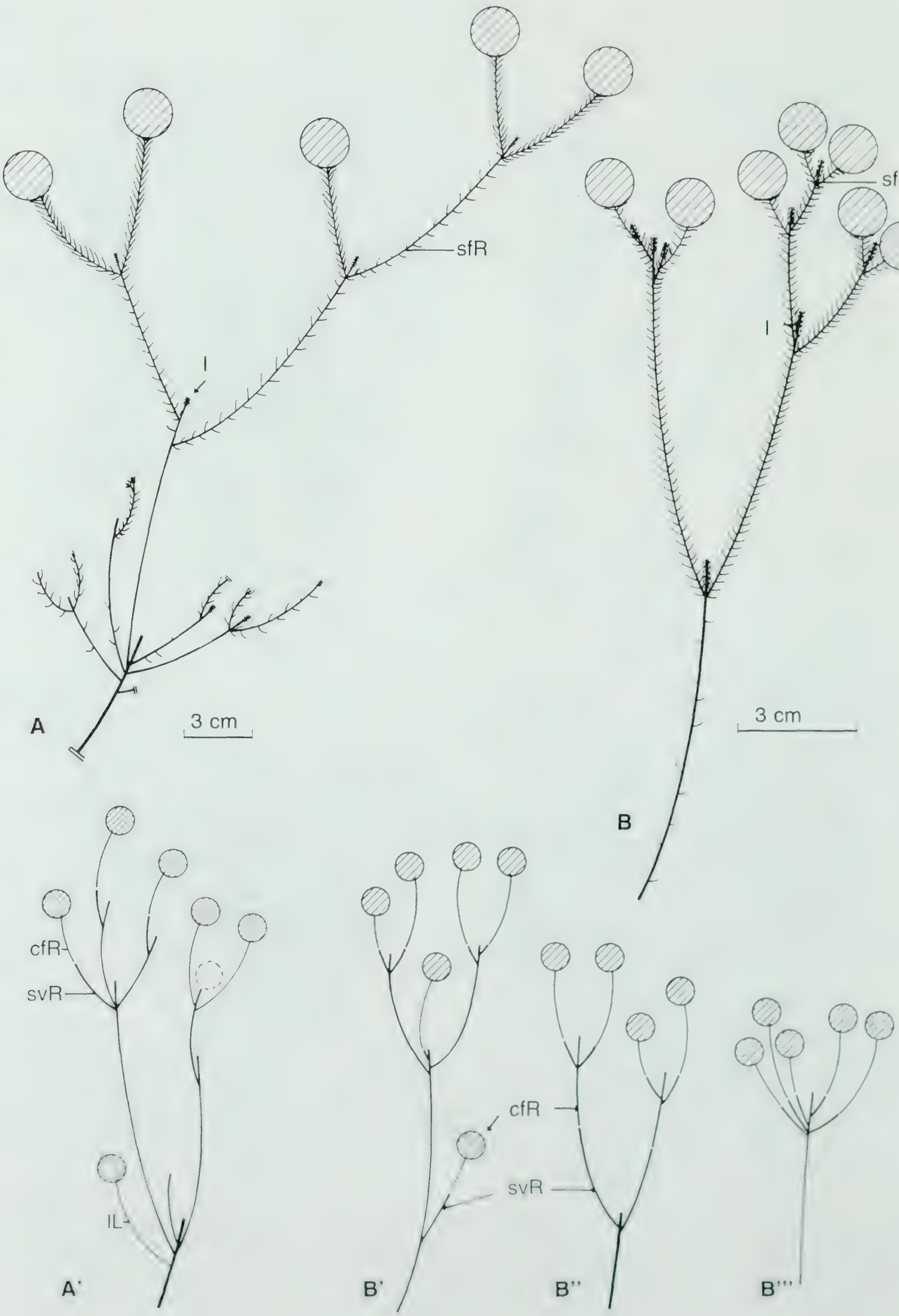


Figure 84 - **Lonchostoma**. *Profiles of* L. myrtoides *(A-A') and* L. pentandrum *(B-B''').* I, *inflorescence axis.*

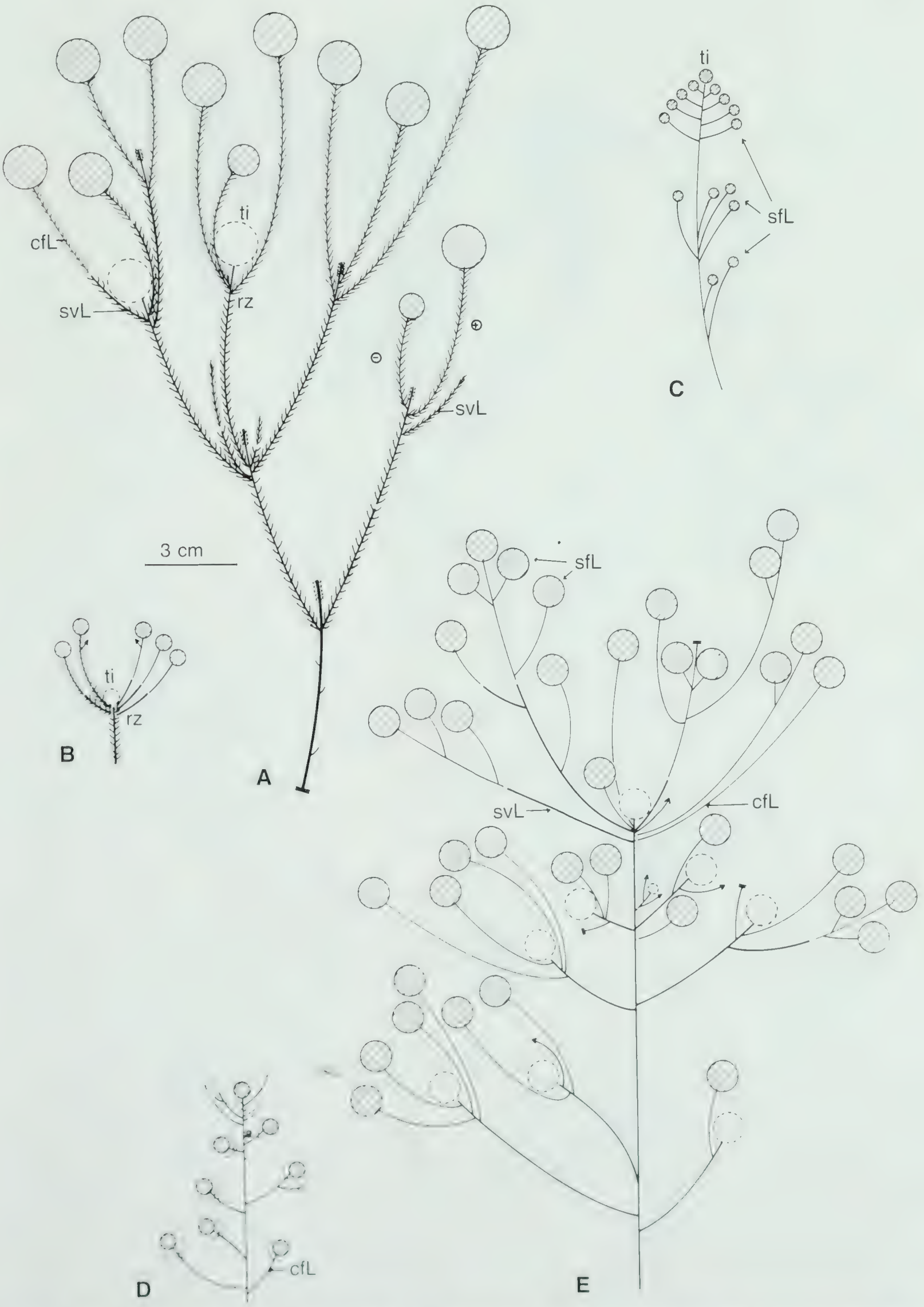


Figure 85 — ***Profiles of* Lonchostoma monogynum** *A-B, most frequent form with terminal inflorescences and renewal shoots below them, C-E, rare form with many sylleptic flowering lateral shoots below the terminal inflorescence, in D the previous season of E is shown. Compare A with fig. 83C.*

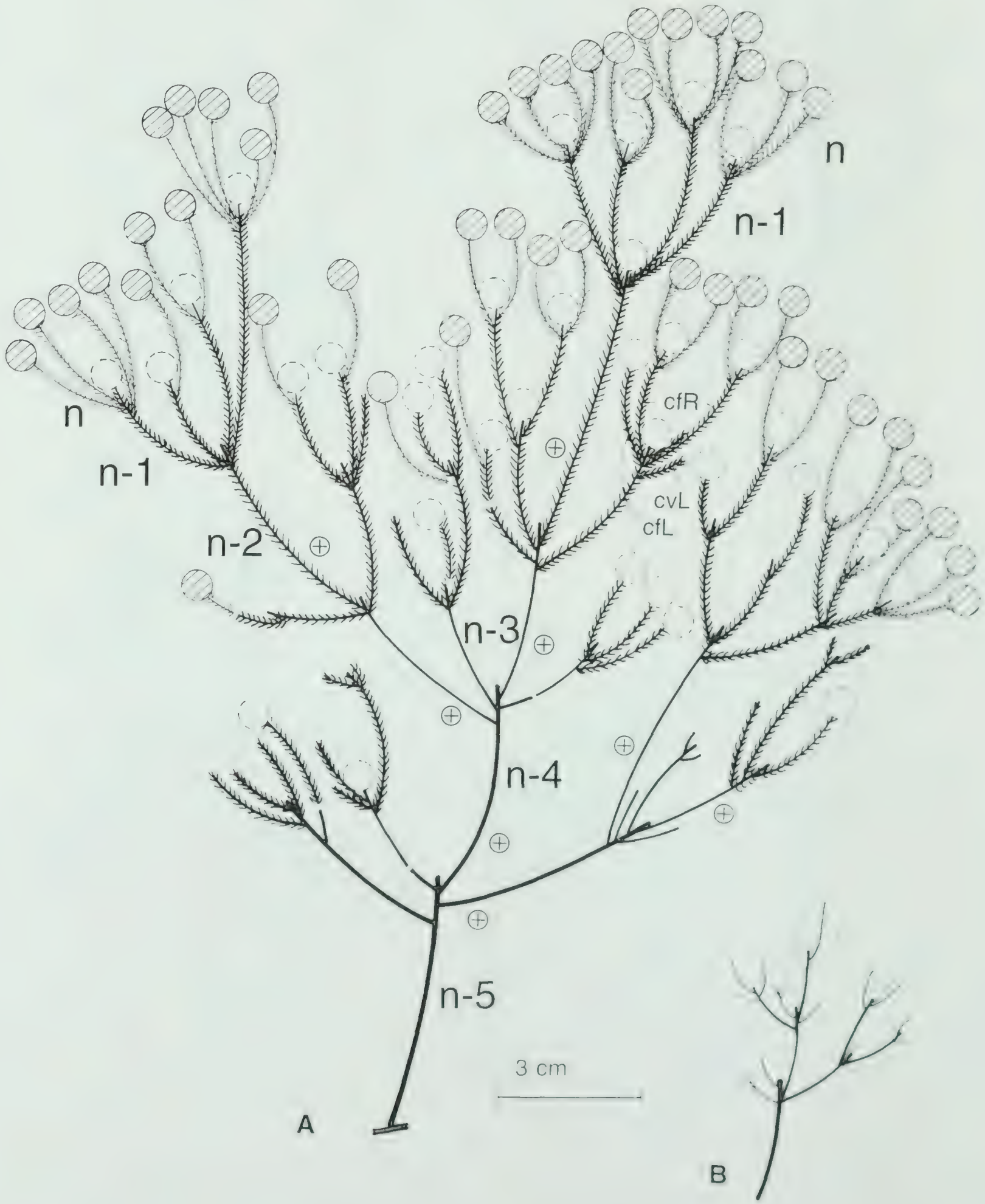
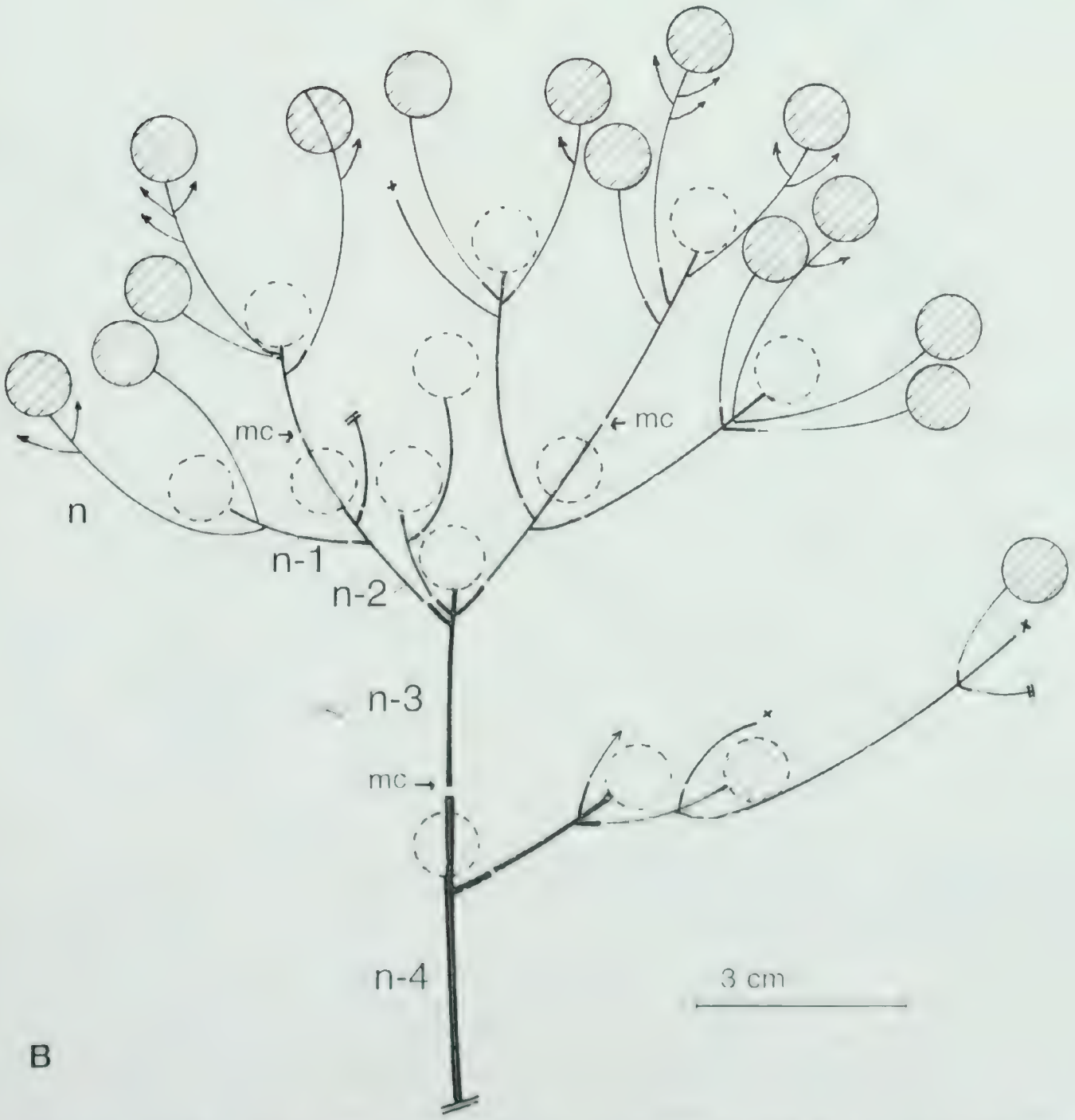


Figure 86 - **Lonchostoma purpureum**. *Profile of a six season old flowering shoot system. In A the thickness of the lines corresponds to the individual SGUs, in B the real growth form is shown*

cvL, *cataleptic vegetative lateral shoot; compare with fig. 83D*

A



B

Figure 87 - **Lonchostoma esterhuyseniae**. *Flowering shoot system (A, Powrie 108, B) and its profile (B), five seasons old. Note that the main axis occasionally protrudes the terminal inflorescence* (mc).

The occasional presence of more than two prophylls, the folious character of the flower-subtending leaves and particularly the unusual growth behaviour of *L. esterhuyseniae* admits of two interpretations of the morphological nature of the inflorescence. (1) The inflorescence is thought to be a terminal truncate cephaloid Then, in *L. esterhuyseniae* the apex of the inflorescence secondarily reactivates and continues to grow (2) The shoot system is compared with *Audouinia capitata* where individual uniflorous short-shoots assemble forming a spike-like inflorescence. Then, the terminal position of the inflorescence and the resulting sympodial growth behaviour of all *Lonchostoma* species except *L. esterhuyseniae* would be secondary.

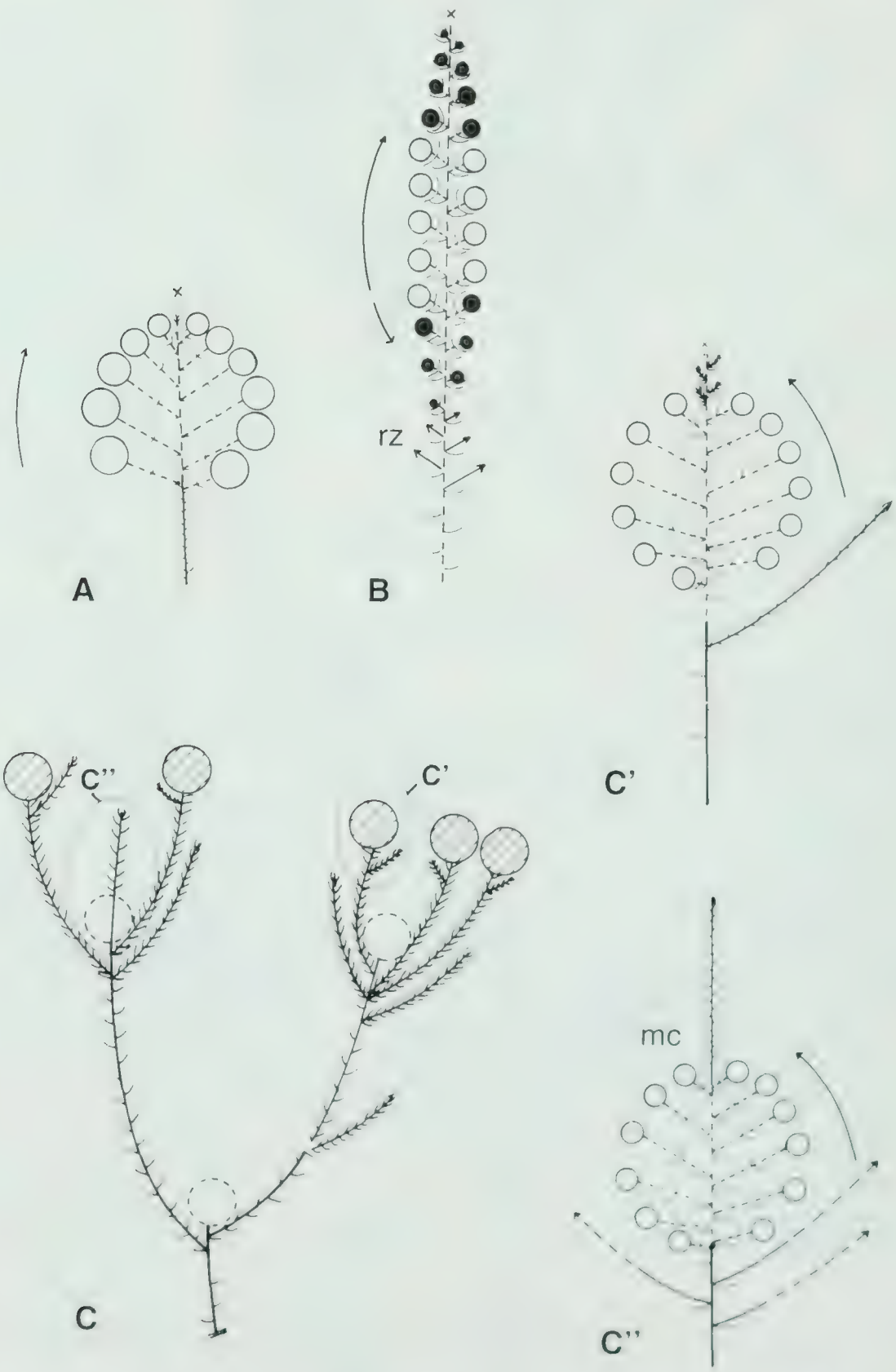


Figure 88 - **Lonchostoma**. *Profiles of the inflorescences of the genus. A*, L. purpureum, *B*, L. monogynum, *C-C''* L. esterhuyseniae: *C, profile of a flowering shoot system, C', inflorescence with an apex dying off, and C'' inflorescence with an apex growing on in the next season. Arrows: flowering sequence.*

Summary. The genus is sympodially branched, that is a new shoot generation is formed in each season As fig 90A shows the RS is subdivided into the zone of insertion (rz-1), the branching zone (bz), the subfloral renewal zone (rz) and the apical zone (az) bearing the terminal inflorescence (ti) The apex always remains open and, with the exception of *L. esterhuyseniae*, dies off after flower production The inflorescence is simple and indeterminate, the flowers are subtended by a leaf and two, in *L. myrtoides*, three prophylls Below the terminal inflorescence the renewal shoots are formed, the remaining part of the sympodium is not branched

The RS varies in different ways: In *L. esterhuyseniae* the apex occasionally continues to grow on and the sympodium then is characterized by a monopodial insert (B: mc). In *L. monogynum* the vegetative zone is occasionally branched showing sylleptic flowering lateral shoots (C: *B*, sfL). In fig. 90D the variations in time which are more or less present in all *Lonchostoma* species are put together. They exclusively concern the renewal zone and manifest themselves in an earlier sprouting (svR) and in an earlier (sfR) or retarded flowering (lL).

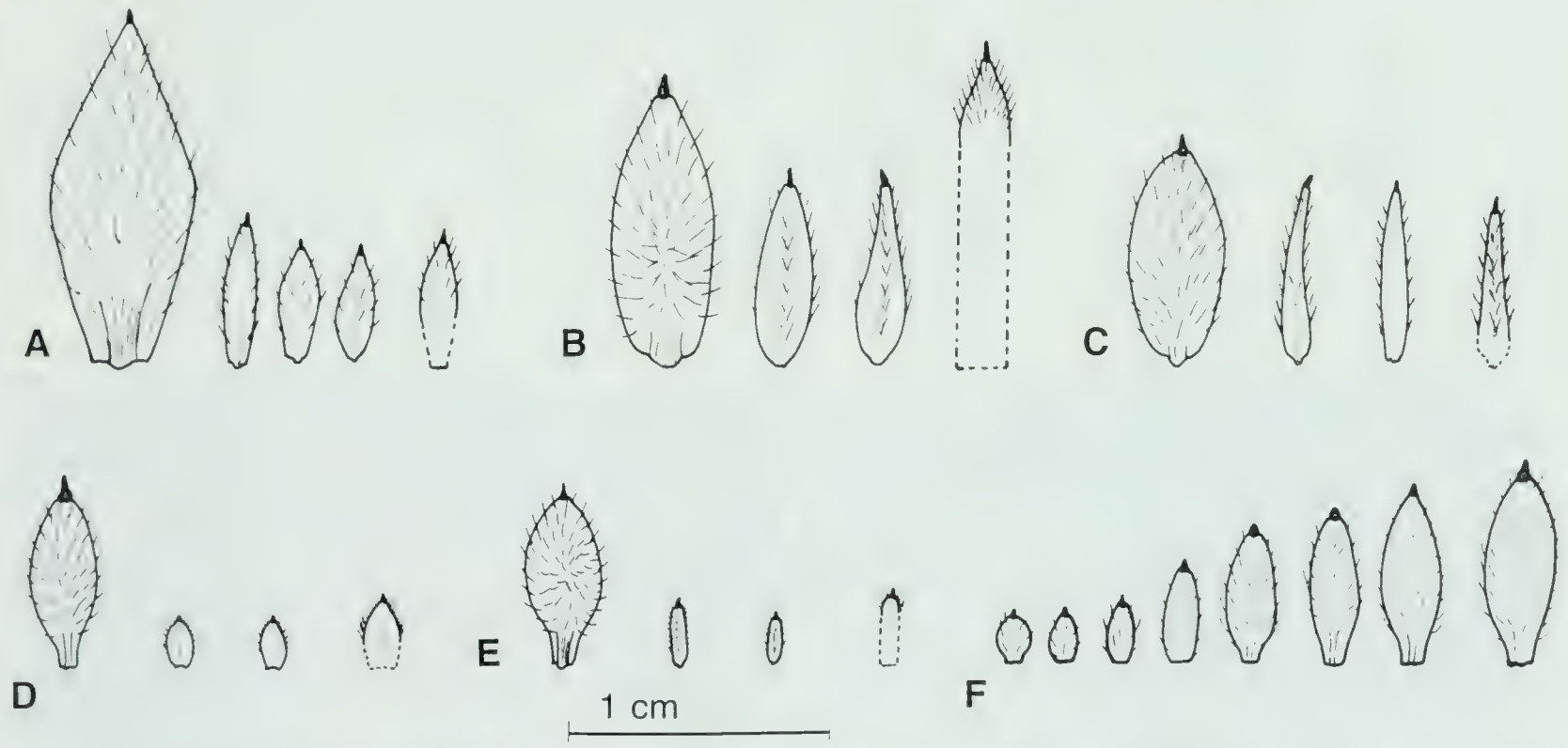


Figure 89 - ***Leaf metamorphosis in the genus*** **Lonchostoma**. *A*, L.myrtoides, *B*, L. esterhuyseniae, *C*, L. monogynum, *D*, *F*, L. pentandrum, *E*, L. purpureum. *A-E, each from left to right: flower subtending leaf, two or three prophylls, sepal, F, foliation at the base of a renewal shoot.*

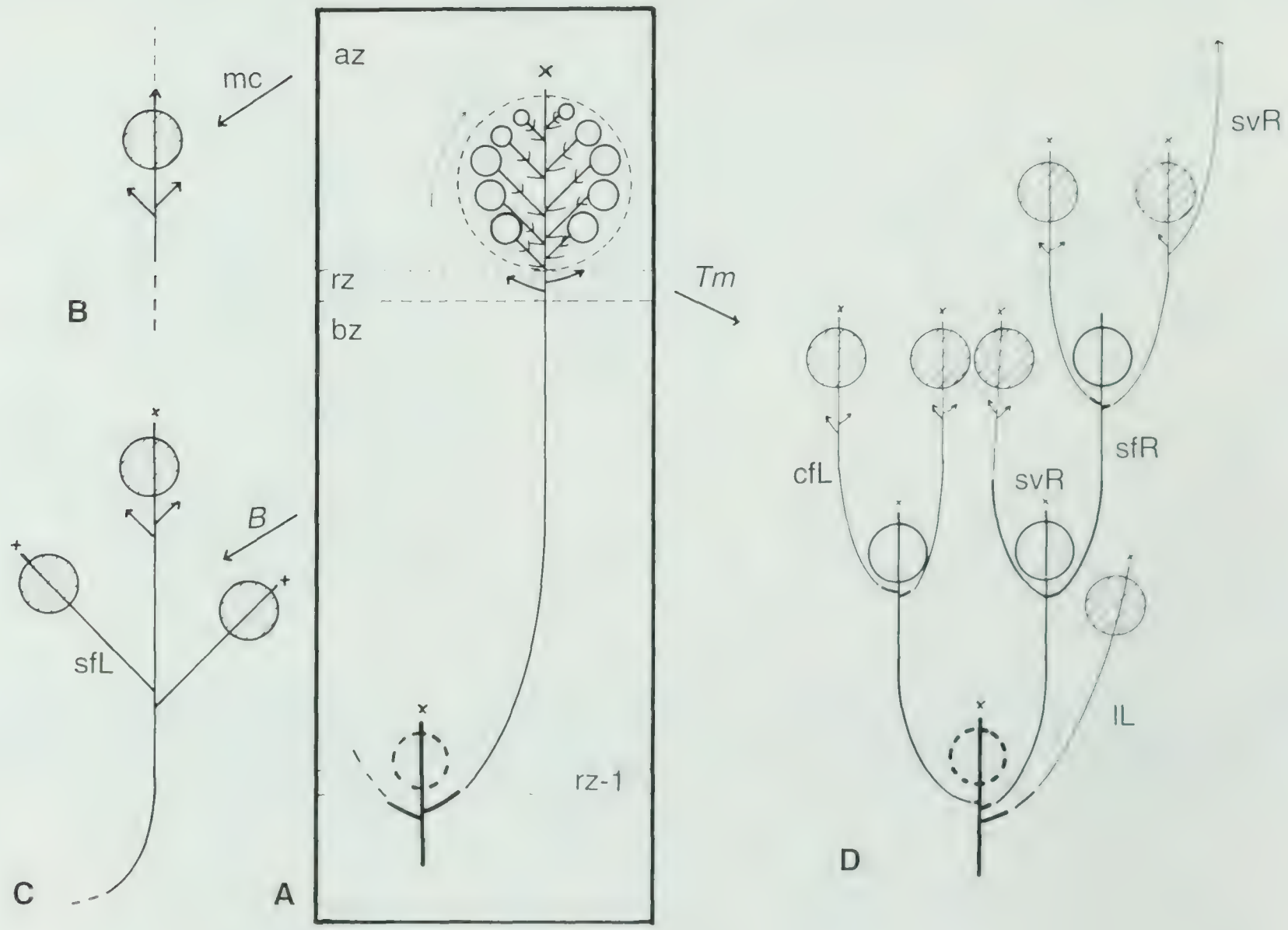


Figure 90 - ***Model of the genus*** **Lonchostoma**. *A, reference system (RS): the apex remains open, the inflorescence is simple, the renewal shoots are present below the inflorescence, the remaining part is unbranched. B-D, variations of the model: B, monopodial units in* L. esterhuyseniae, *C, sylleptic flowering lateral shoots in* L. monogynum *and* L. esterhuyseniae, *D, variation in time shown by all species.*

B, branching, IL, *late lateral shoot, Tm, shifting in time.*

3.6 ***Mniothamnea*** Niedenzu

The genus has only two rare species, M. callunoides *is an erect shrub growing in dense shrubland (Scott, pers. comm.).* M. bullata *grows between rocks and shows a more or less creeping habit. Two individuals of* M. bullata *have been found in the Langeberg, forming mats between the rocks at the summit of Grootberg (5300 ft).* M. callunoides *has been analyzed from herbarium specimens.*

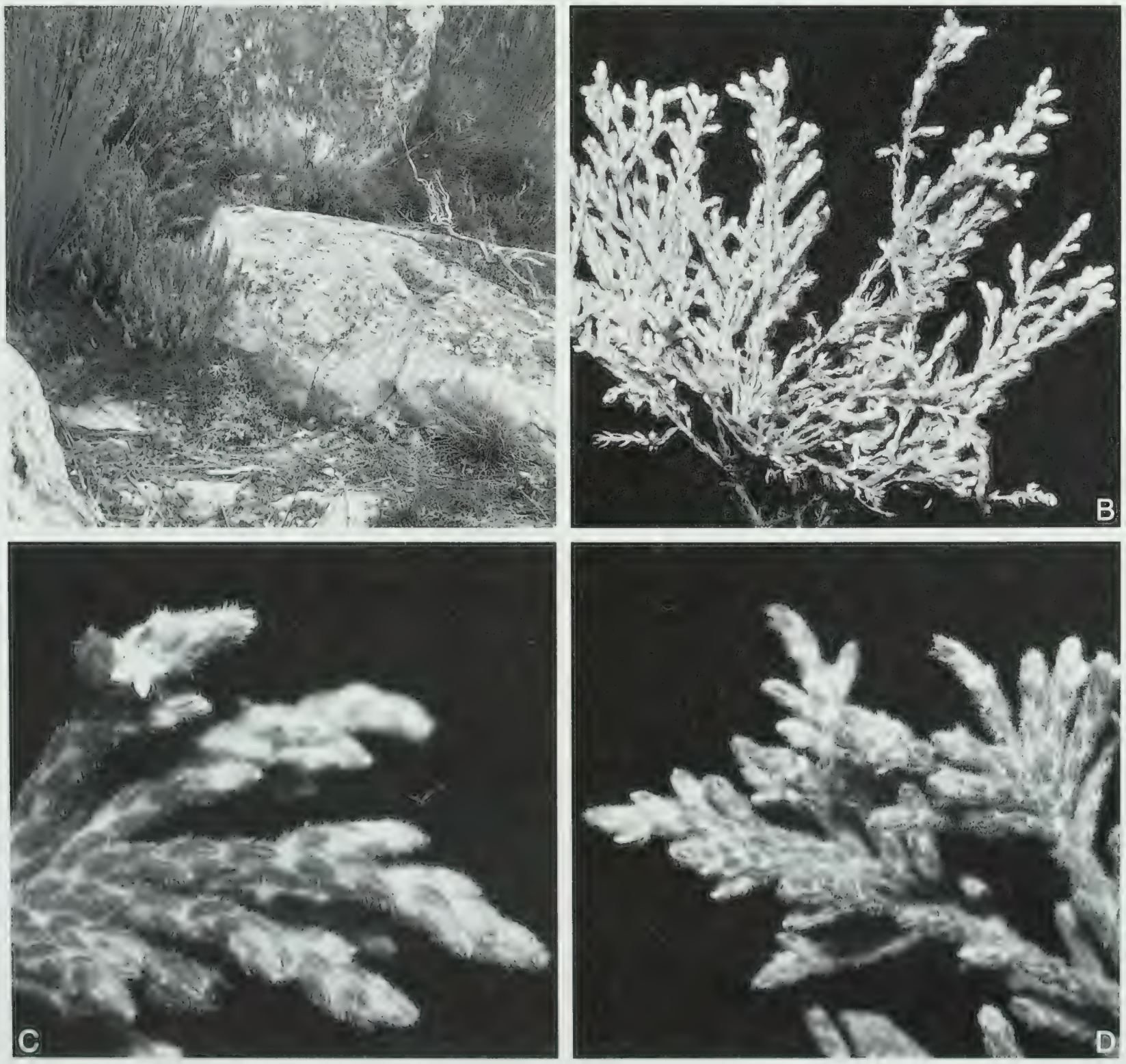


Figure 91 - **Mniothamnea bullata**. *A, locality between rocks at the top of Grootberg (5300 ft), B-D, habit of a shoot systems, in C with a minute flower of about 2 mm in diameter*

Growth and branching pattern. Both species of *Mniothamnea* show a variable habit ranging from low compact mats (fig. 95A) to long and slender shoot systems (fig. 95C). As in other genera of Bruniaceae, the nature of the leaf and stem surface assists in delimiting the individual SGUs in *Mniothamnea*. The densely appressed leaves persist for at least three seasons. The young leaves are green and densely covered with silvery hairs (fig. 91C), becoming harder in texture and darker in colour with age until they are shed as glabrous, greyish-brown organs (fig. 91B).

In *M. bullata* the mode of branching obviously depends on the position of the shoots. As fig. 92A demonstrates, the horizontally spreading shoots are often connected in a monopodial manner (mc) while the erect shoots tend to branch in a sympodial manner. The renewal shoots, being arranged in a subterminal zone (fig. 93A′: rz), very often grow out sylleptically, pass into a resting phase and continue to grow the following season (fig. 93A′, 94A: sR).

The individual SGUs are much-branched. An exact analysis of the nature of the lateral organs is difficult because the primordia of the vegetative shoots, the flower buds and the deflorated flowers are all minute and covered by hairy leaves (fig. 91C,D, 94A′). However, the flower-leaf complex is somewhat larger than the vegetative primordium of a lateral shoot. This slight difference in size underlies the profiles shown in fig. 92-94. Only the profile in fig. 92B has been analysed in detail by preparing each primordium under the binocular microscope. It confirms the arrangement of flowers shown in the remaining profiles.

The dominant shoot of an individual SGU may end in a terminal flower or remain vegetative, dying off or growing on in the next season. The lateral shoots may remain vegetative (fig. 92B: svL) or have flowers of 1st to 3rd order of branches (fig. 94A: I-III). The flowers may be densely arranged and resemble a few-flowered inflorescence, but are nearly always separated from each other by sterile leaves (fig. 94A′). The flowering shoots are branched and determinate (fig. 92B: dL) or indeterminate (iL). In the latter case the shoots may, as is the case of the main axis, grow on in the next season (fig. 94A: mc′).

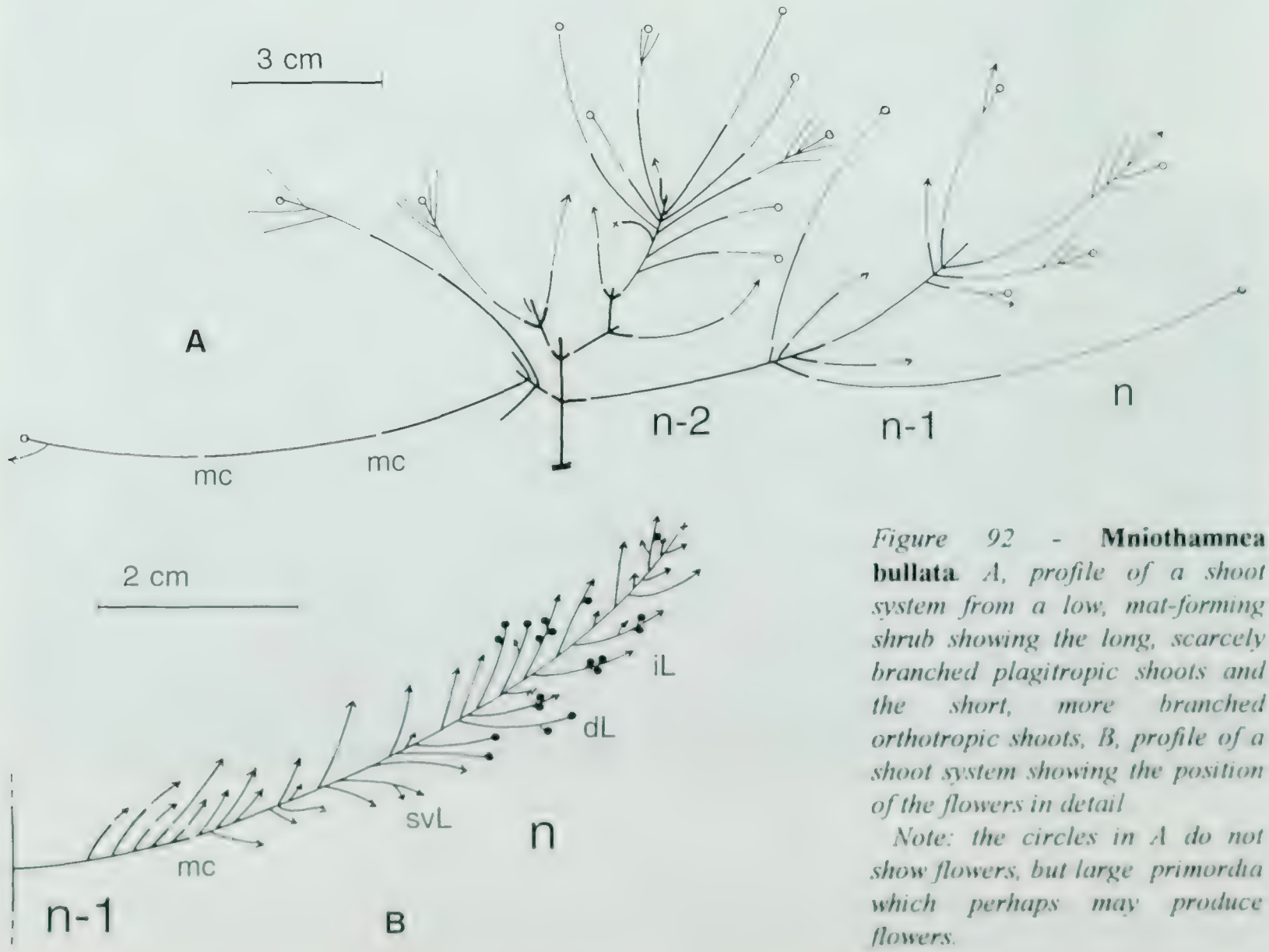


Figure 92 - **Mniothamnea bullata**. *A, profile of a shoot system from a low, mat-forming shrub showing the long, scarcely branched plagitropic shoots and the short, more branched orthotropic shoots, B, profile of a shoot system showing the position of the flowers in detail*

Note: the circles in A do not show flowers, but large primordia which perhaps may produce flowers.

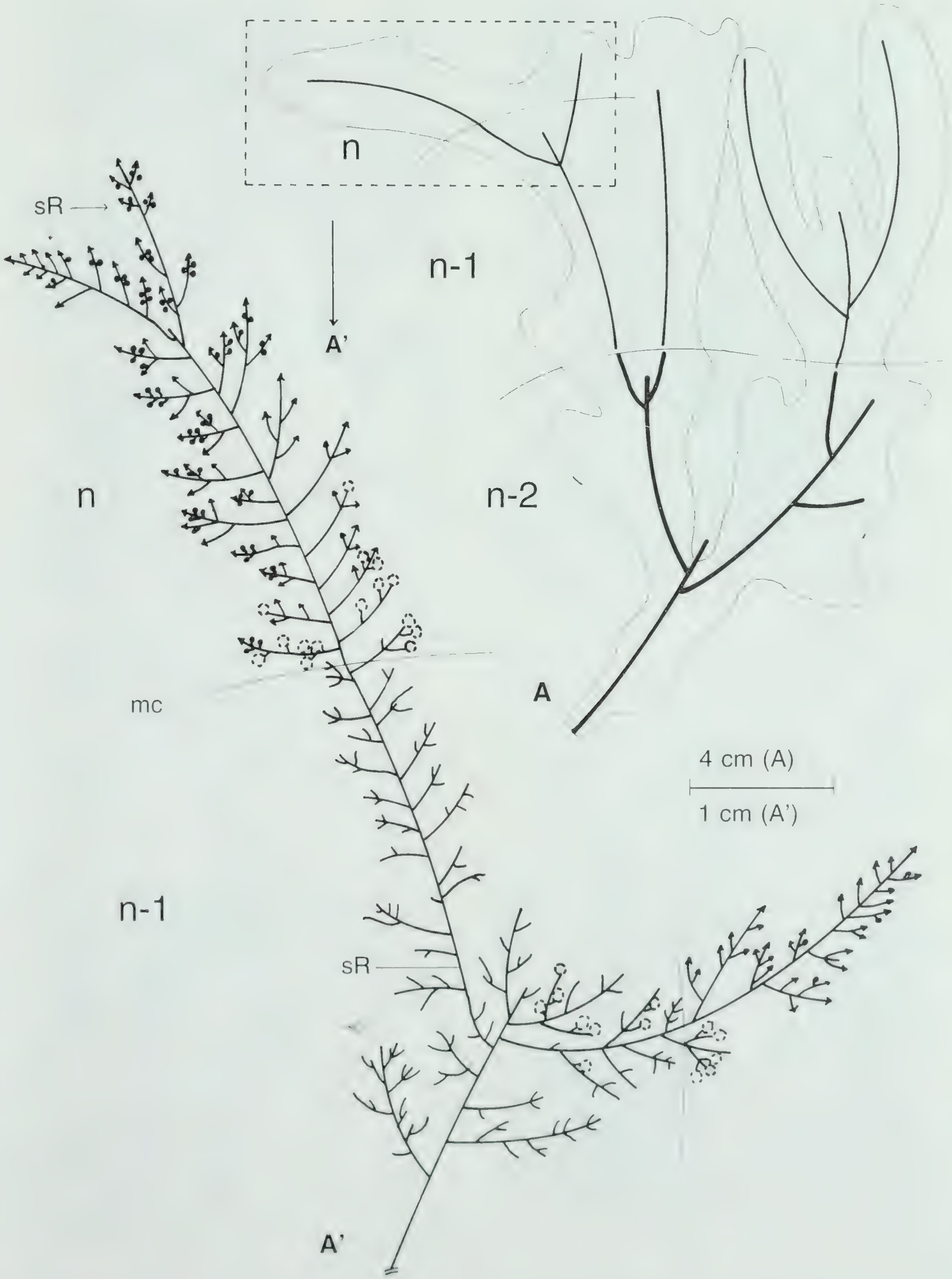


Figure 93 - **Mniothamnea bullata**. *A, branching pattern of a shoot system, three seasons old, A', detail from A.* sR, *sylleptic renewal shoot; compare with fig. 95A*

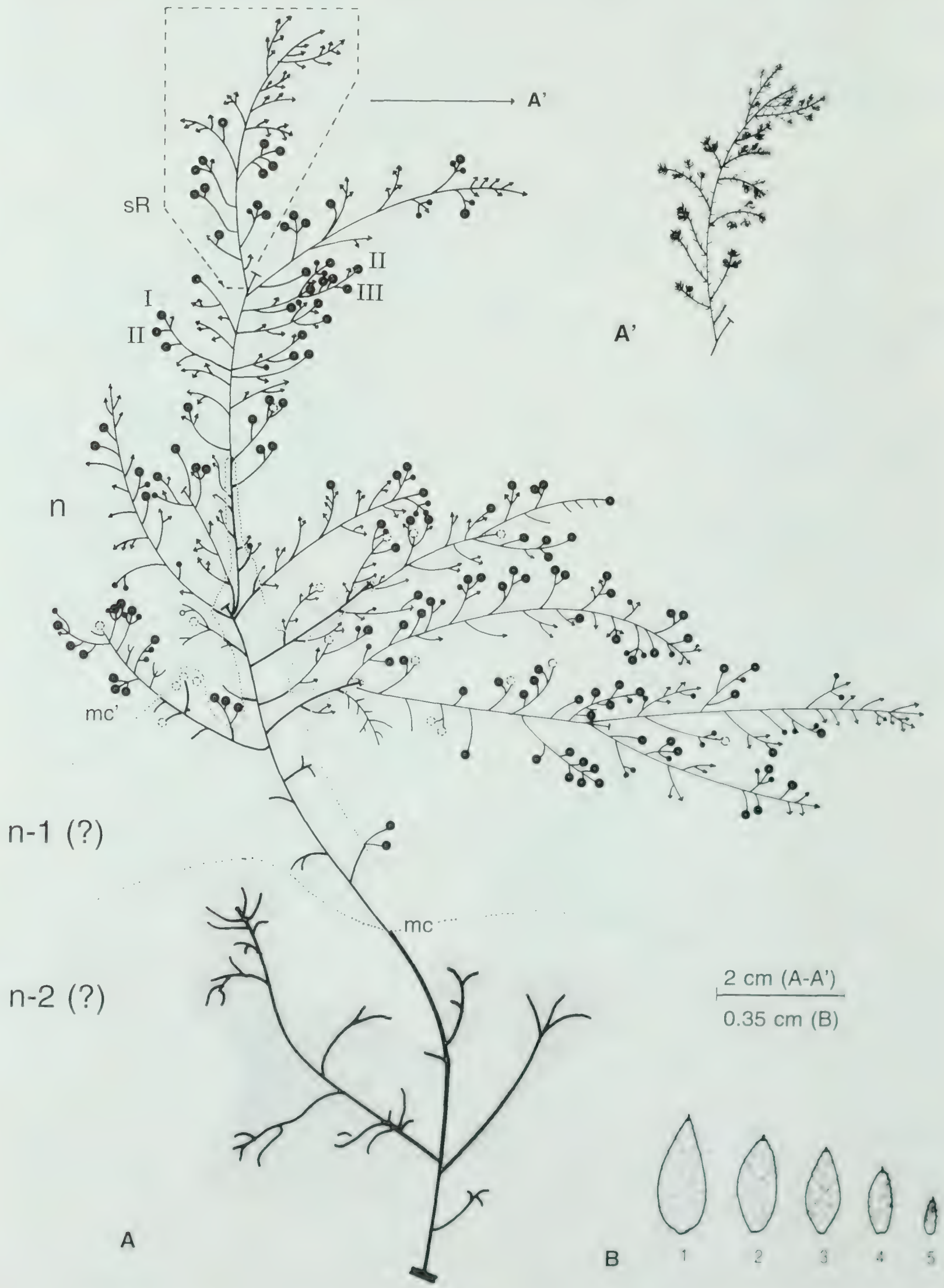


Figure 94 - **Mniothamnea bullata**. *A, profile of a flowering shoot system, probably three seasons old, A', detail from A, illustrating the moss-like habit of the branches and the difficulty in distinguishing between vegetative and reproductive primordia. (All flowers are in the postfloral stage and only for reasons of clarity drawn in solid black). B, leaf metamorphosis showing the gradual transition from foliage (1) to floral leaves (5).*
sR, sylleptic renewal shoot; compare with fig. 95B

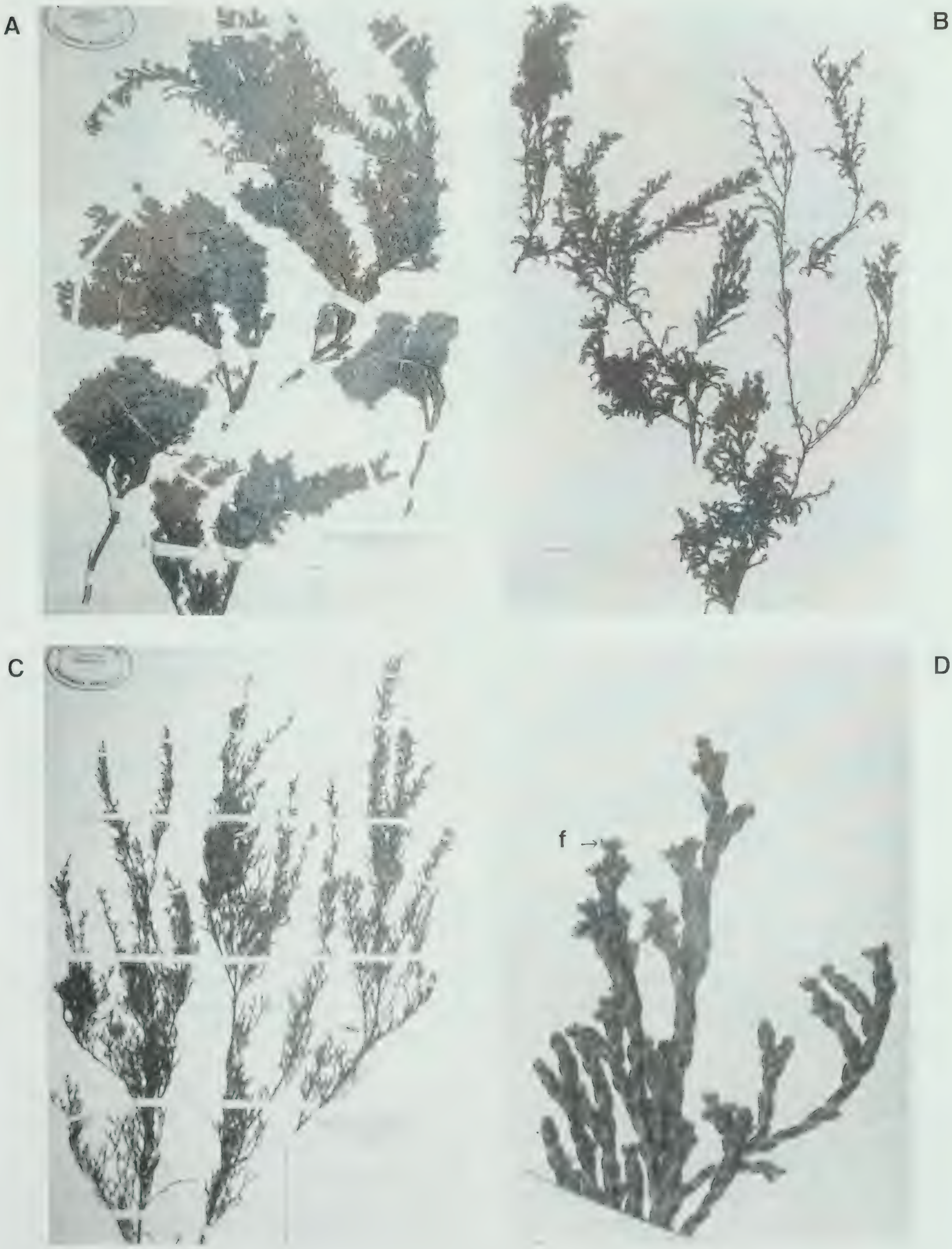


Figure 95 - **Mniothamnea**. *Flowering shoot systems of* M. bullata *(A; Rourke 628, NBG, B; Carlquist 4715, B) and* M. callunoides *(C,D; Rourke 1289, NBG). Note the moss-like habit and the minute flowers in D.*
f, *flower; compare A with fig. 93, B with fig. 94A, and C with fig. 96.*

M. callunoides (fig. 95C,D) is characterized by a more upright growth habit than *M. bullata* (Pillans 1947:168). As fig. 96A demonstrates, a sympodial branching pattern with distal renewal zones dominates the erect shoot systems. It is presumed that the individual sympodial units have a lifespan of more than one season as is shown in fig. 97A. In general, however, it is more difficult to delimit the individual SGUs in this species than in *M. bullata*, because leaf metamorphosis is less obvious with age.

The profiles of selected shoot systems shown in fig. 96A´ and 97A illustrate the variability of the branching pattern and flower arrangement.

In fig. 97A a short shoot system about five centimeters in length is illustrated. It is presumed to be three seasons old, with the individual SGUs being connected in a monopodial manner. The lateral shoots are either unbranched and terminating in a flower (I), or branched and determinate (dL) with flowers of 1st and 2nd order, or entirely vegetative but growing on in the next season (svL).

In contrast, unbranched and determinate flowering shoots are largely lacking in the shoot system shown in fig. 96A´. The lateral flowering shoots are predominantly indeterminate (iL) with several sessile or shortly petiolated flowers of 2nd order in their distal part (II) and either vegetative shoots or indeterminate flowering shoots of 2nd order with flowers of 3rd order (III) in their proximal part. Within the basal part of the shoot system illustrated, an age gradient is present (*, **) between some flowers. However, whether this gradient indicates two different seasons or not is unknown.

It is also unclear whether the main axis of an individual SGU always remains open or may produce a terminal flower.

Leaf metamorphosis and inflorescence structure. According to Pillans (1947:168) the flowers of *Mniothamnea* are `terminal or axillary´ and `subtended by 2 bracteoles´. These statements are subject to certain qualifications:

The phenomenon of leaf metamorphosis shows that in both species green photosynthetic leaves are present immediately below the flowers (fig. 94B, 97B). Below each flower, up to five leaves may be present; these differ in size from the stem leaves and may be called transitional leaves (fig. 94B: 2-5, 97B: 2-6). Depending on the length of the flowering shoots, these transitional leaves appear either above the stem leaves or unaccompanied by them, sometimes in a reduced number. Thus, leaf metamorphosis is more or less abrupt. In the extreme case of a shortly petiolated flowering shoot, only two leaves are present which are markedly smaller than the remaining leaves. Obviously this is the example Pillans referred to as an `axillary flower subtended by two bracteoles´. In fact, there is no fundamental difference between a `terminal´ and an `axillary´ flower, because all transitional arrangements are present. Likewise the presence or absence of two bracteoles depends only on the length of the shoot, which always ends in a terminal flower.

In conclusion, it seems to be more feasible to regard the individual flowers of *Mniothamnea* as equal to each other, but arranged at the ends of shoots which differ in length and order of branching. This would be compatible with a tendency for several one-flowered short-shoots to form a cluster that superficially resembles a simple inflorescence (fig. 96A´). Each flower is then subtended by two to four transitional leaves and separated form the next flower by sterile leaves which appear in variable number among individual flowers.

Summary. Fig. 98 summarizes the morphological data analyzed for the genus *Mniothamnea*. For comparison the reference system (RS) is shown in A and its variations in B-D.

The dominant shoot ends in a terminal flower (tf) or in a vegetative apex which either dies off or grows on in the next season (mc). Below the apical zone (az), renewal shoots appear (rz) and may start to grow out sylleptically. The whole branching zone (bz) is sylleptically branched. Vegetative and reproductive shoots may be either determinate (dL) or indeterminate (iL) and vary as to their number and position. A schematic survey on the different kinds of lateral shoots is given in fig. 98A. The individual flowers appear terminally at shoots of 1st to 3rd order branches (I-III) and are either separated from each other or homogenized and aggregated in inflorescence-like clusters.

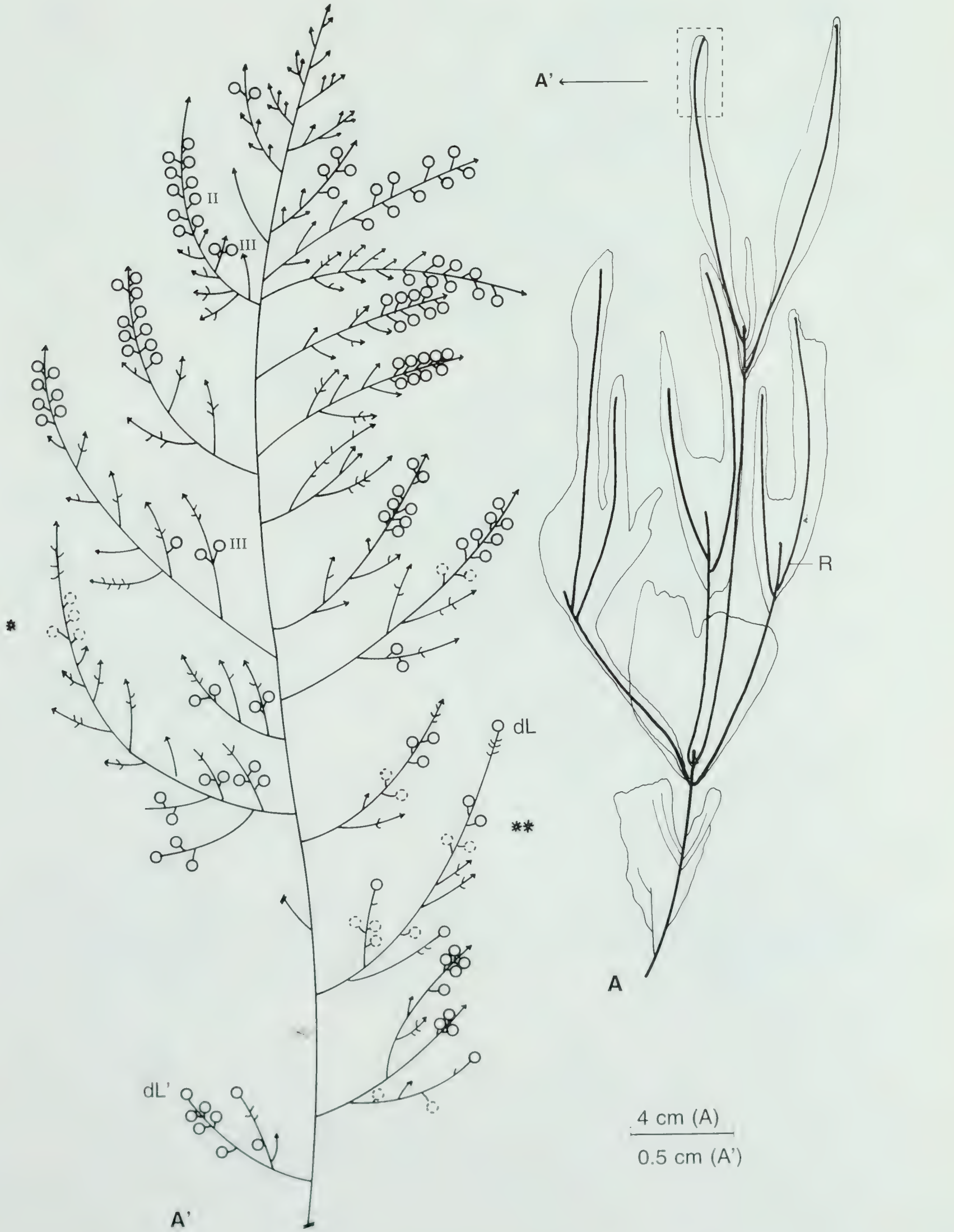


Figure 96 - **Mniothamnea callunoides**. *A, branching pattern of a shoot system showing the sympodial habit of the shoot systems, A', detail from A, showing the lateral branches and the arrangements of flowers in detail. *, **, lateral flowering shoots with a clear age gradient between the flowers; compare with fig. 95C.*

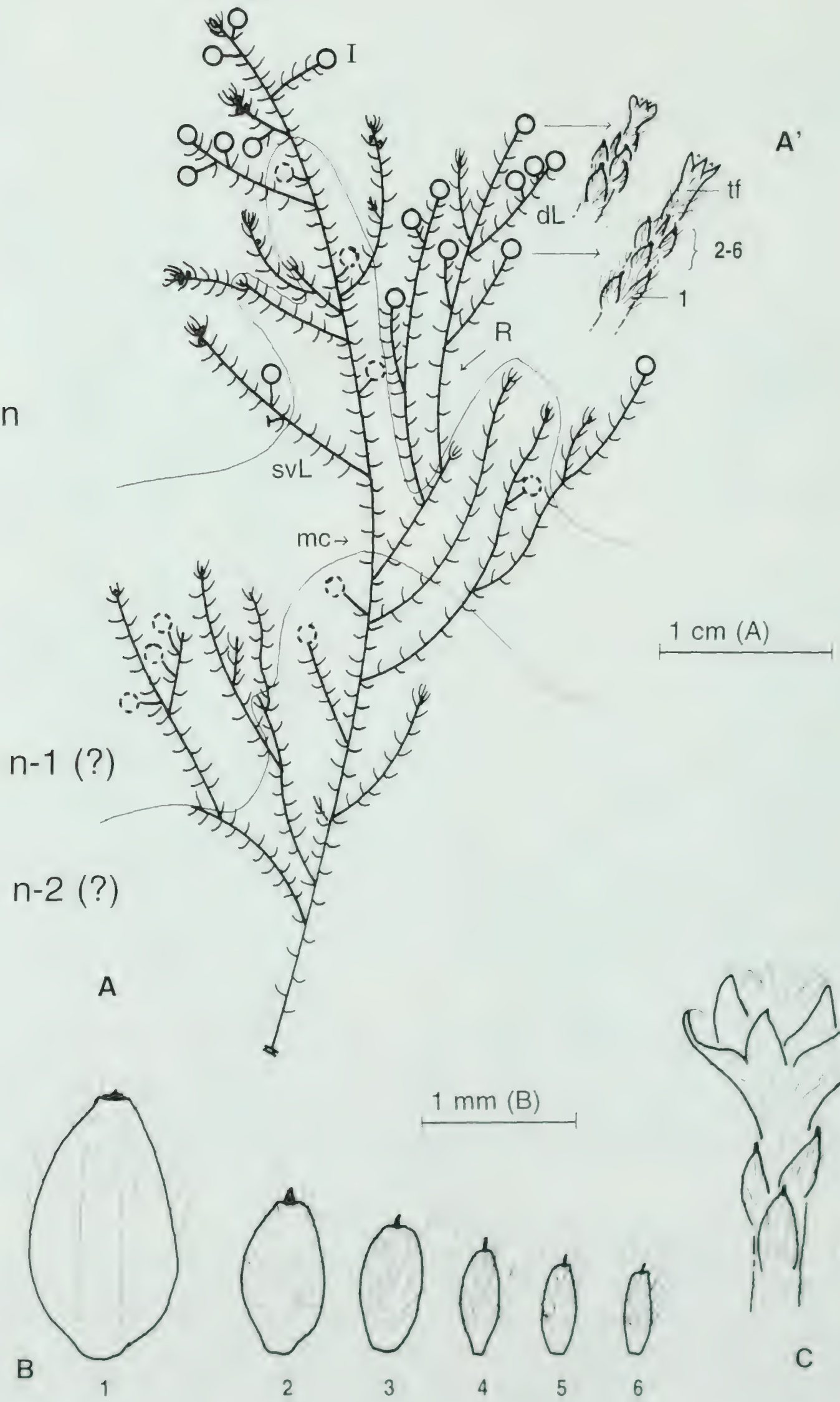


Figure 97 - **Mniothamnea callunoides**. *A, profile of a flowering shoot system, probably three seasons old, A', habit of terminal flowers and leaves below, B, leaf metamorphosis: 1, leaf at the main axis, 2-6, leaves at a flowering shoot showing the decrease in length, C, terminal flower (tf) with leaves immediately below*
The numbers in B correspond to the numbers in A' and C

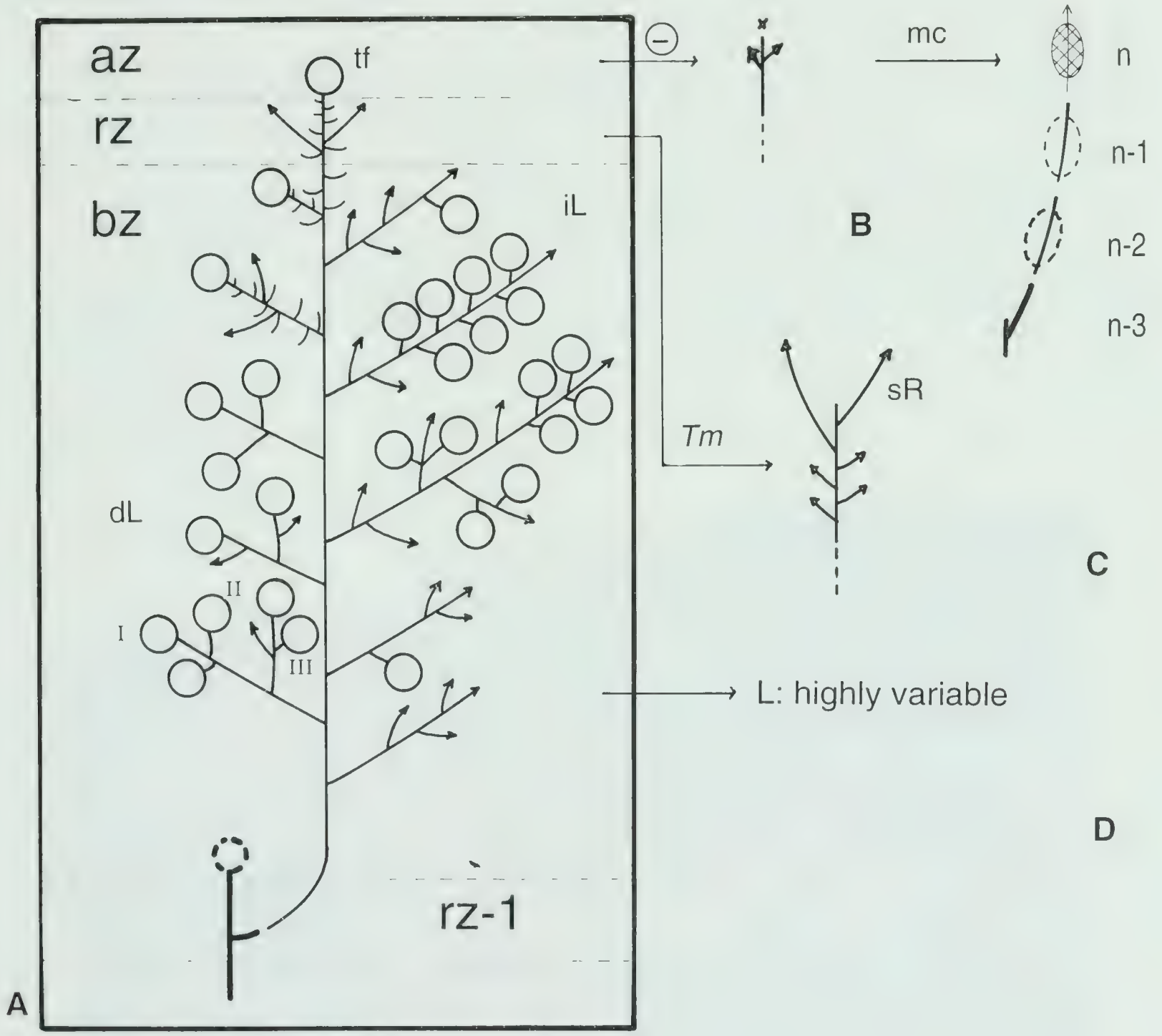


Figure 98 - ***Model of the genus*** **Mniothamnea**. *A, the reference system (RS) of the genus showing the terminal flower, the renewal zone below and the extended branching zone with vegetative and reproductive, determinate and indeterminate lateral shoots (in an artificial arrangement), B-D, variations of the RS as regards the absence of the terminal flower and the growing activity of the apex (B), the precurrent development of the renewal shoots (C) and the high variability of the branching zone (D).*

sR, *sylleptic renewal shoot, Tm, shifting in time.*

3.7 ***Nebelia*** Neck. ex Sweet

The genus comprises six species, concentrated in the Western Cape Province. All species grow as medium-sized erect shrubs. N. fragarioides *and* N. stokoei *are characterized by compound inflorescences (fig. 100).*

N. paleacea *was studied at Sir Lowry's Pass, in the Nuweberg Forest Reserve, in the Vogelgat Nature Reserve and at Landrostkop,* N. fragarioides *was seen at Mount Lebanon, in the Kogelberg Nature Reserve and in the Jonkershoek Nature Reserve. The latter locality, part of a restioid-ericoid fynbos community, was characterized by the presence of many young seedlings.* N. sphaerocephala, N. laevis *and* N.stokoei *were analyzed from herbarium specimens (compare with Claßen-Bockhoff 1995b).*

Figure 99 - **Nebelia fragarioides.** *Restioid-ericoid fynbos community below the summit of Victoria Peak (Jonkershoek Nature Reserve, 3700 ft.) with several flowering shrubs of about 80 cm in height and many young seedlings (November 1987).*

Growth and branching pattern. Adult shrubs of *N. fragarioides* are much-branched and characterized by large pincushion-like inflorescences (fig. 99,100). As different age classes were studied it was possible to reconstruct the life cycle of *N. fragarioides:*

Fig. 107A shows the habit of a seedling, the corresponding profile being given in fig. 101A. The erect apparently monaxial dominant shoot is in fact composed of three shoots: the primary shoot (fig. 101A: P) and two successive renewal shoots (cR) each of which continue the orthotropic growth of the mother axis in a pseudomonopodial manner.

Early development of a much-branched vegetative crown appears to be the rule in this species. During its 1st season the primary shoot becomes sylleptically branched along its whole length of about ten centimeters (fig. 101A: n-2). While the apex dies off, lateral branching continues in the following seasons, resulting in a dense system of relatively short shoots. The lateral primordium immediately below the apex forms the renewal shoot, which develops in a cataleptic way (fig. 101A, n-1: cR). This renewal shoot also branches sylleptically but its main function appears to be to grow in the length.

Below the apex of the renewal shoot, some cataleptic shoots arise, the most-vigorous starting to flower at the end of the 3rd season (fig. 101A, n: cR) while the remainder enhance the vegetative shoot system. Below the compound terminal inflorescence (fig. 101B: tia), numerous inhibited primordia are present (ipi). These appear to mark the transitional zone between the reproductive and the vegetative part of the shoot system since sylleptic vegetative lateral shoots are found immediately below this zone (fig. 101B: svL).

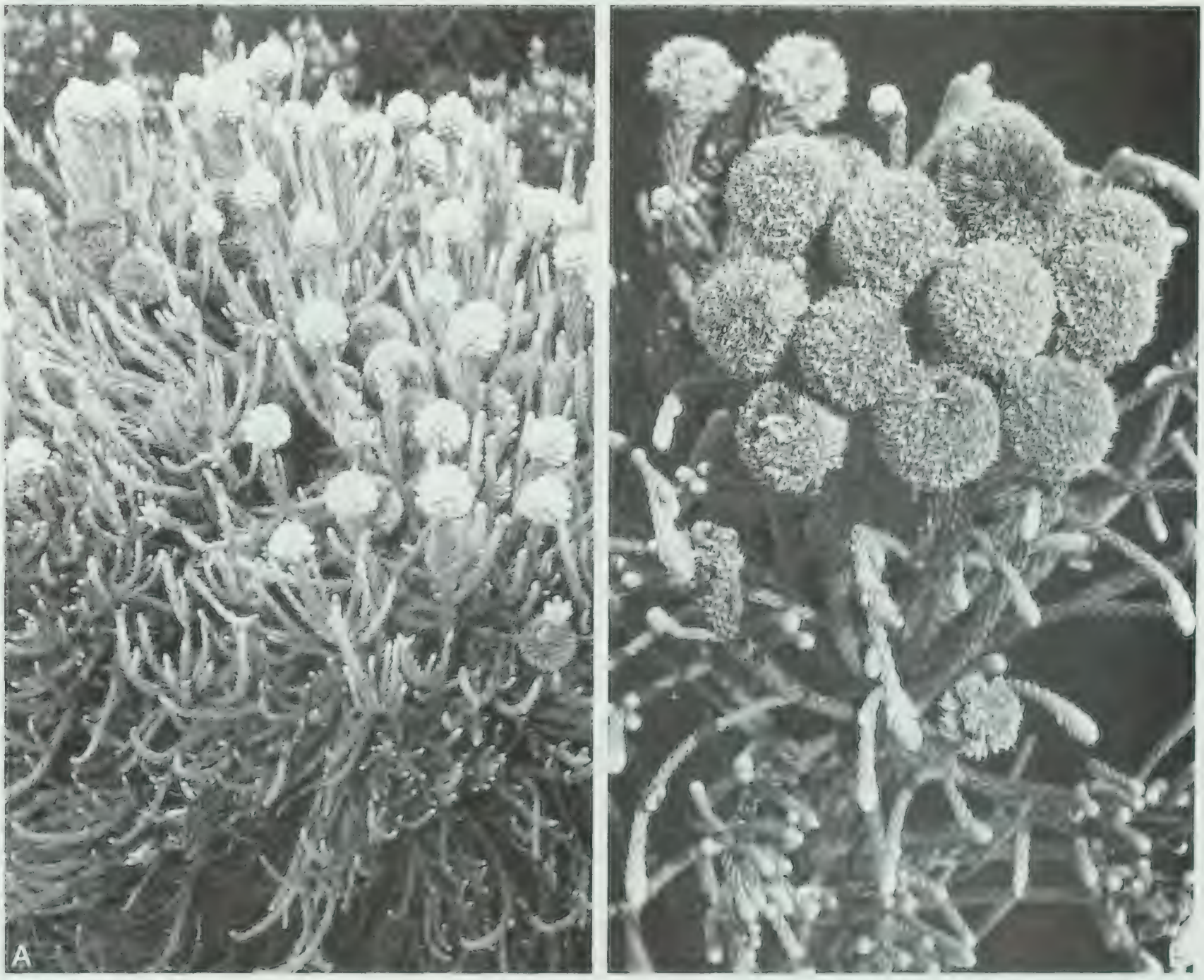


Figure 100 - **Nebelia fragarioides**. *Flowering shoot systems: A, in the prefloral stage, clearly showing the compound nature of the inflorescences, B, in the early postfloral stage, showing the pincushion-like habit of the inflorescences.*

Shoot systems of young plants about 60 cm high are shown in fig. 102 and fig. 103. Active vegetative growth is the most characteristic attribute of this age class. The apex may die off as in the seedling with the shoot system being extended sympodially by up to five subterminally arranged renewal shoots (fig. 102, n-1: R). Alternatively, the apex may continue to grow on in the next season, connecting the SGUs in a monopodial way (mc). The shoot system is then enhanced by up to ten additional lateral shoots arising from the base of the new season's growth (sL). The vegetative shoot system of the shrub rapidly extends. Owing to the still predominating juvenile sprouting activity within the shoot system, only a few shoots come to flower to form a terminal or occasionally an additional lateral inflorescence (fig. 103B). The renewal shoots very often arise from the middle part of the flowering shoot, thus exhibiting marked mesotony.

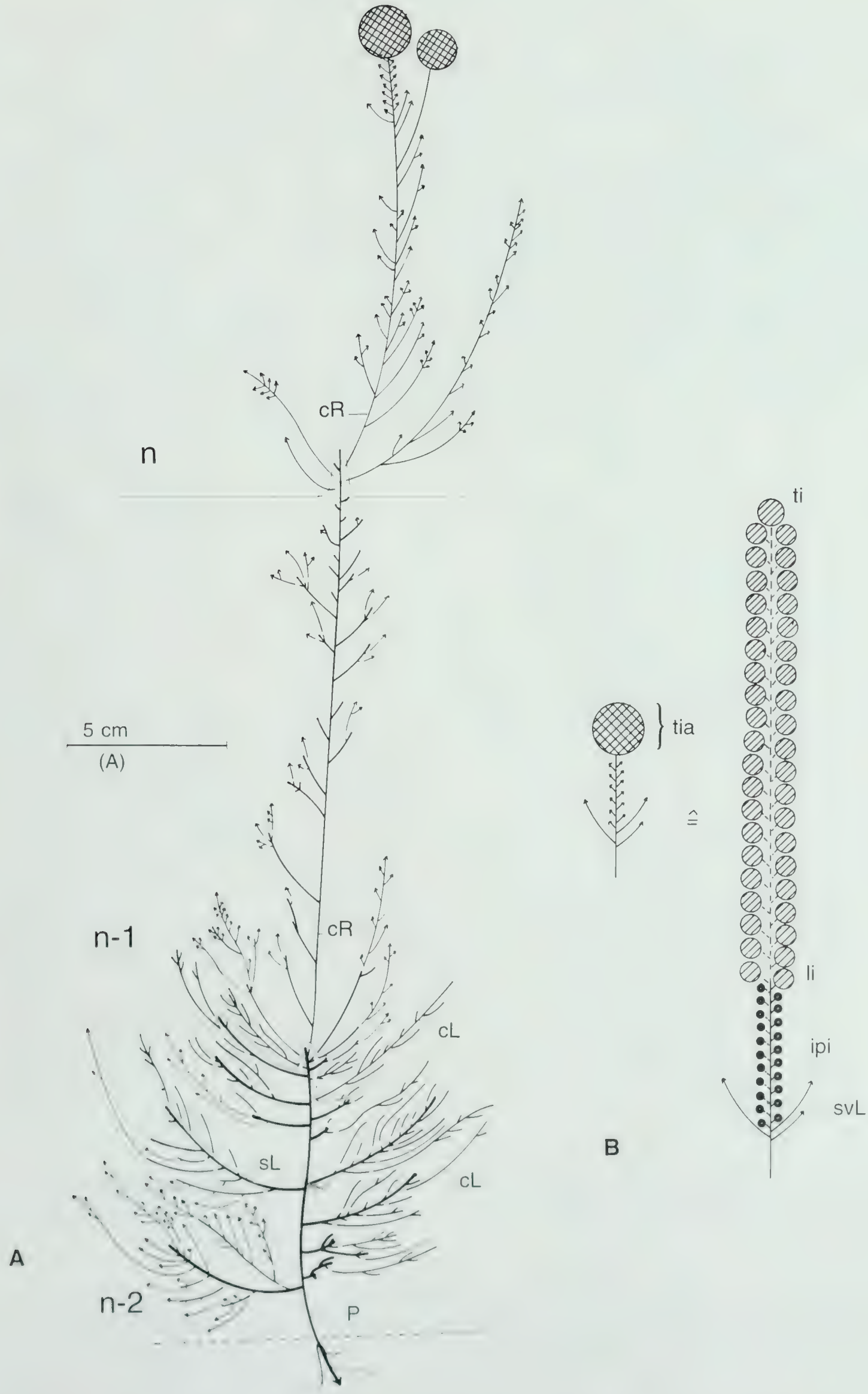


Figure 101 - **Nebelia fragarioides**. *A, profile of a seedling, three seasons old (compare with fig. 107A). In the first season a richly branched vegetative shoot system is formed, in the second season the shrub increases in height and in the third season it starts to flower. B, profile of the compound inflorescence with an inhibition zone below the proximal lateral inflorescences.*

cL, *cataleptic lateral shoot*, P, *primary axis*, sL, *sylleptic lateral shoot.*

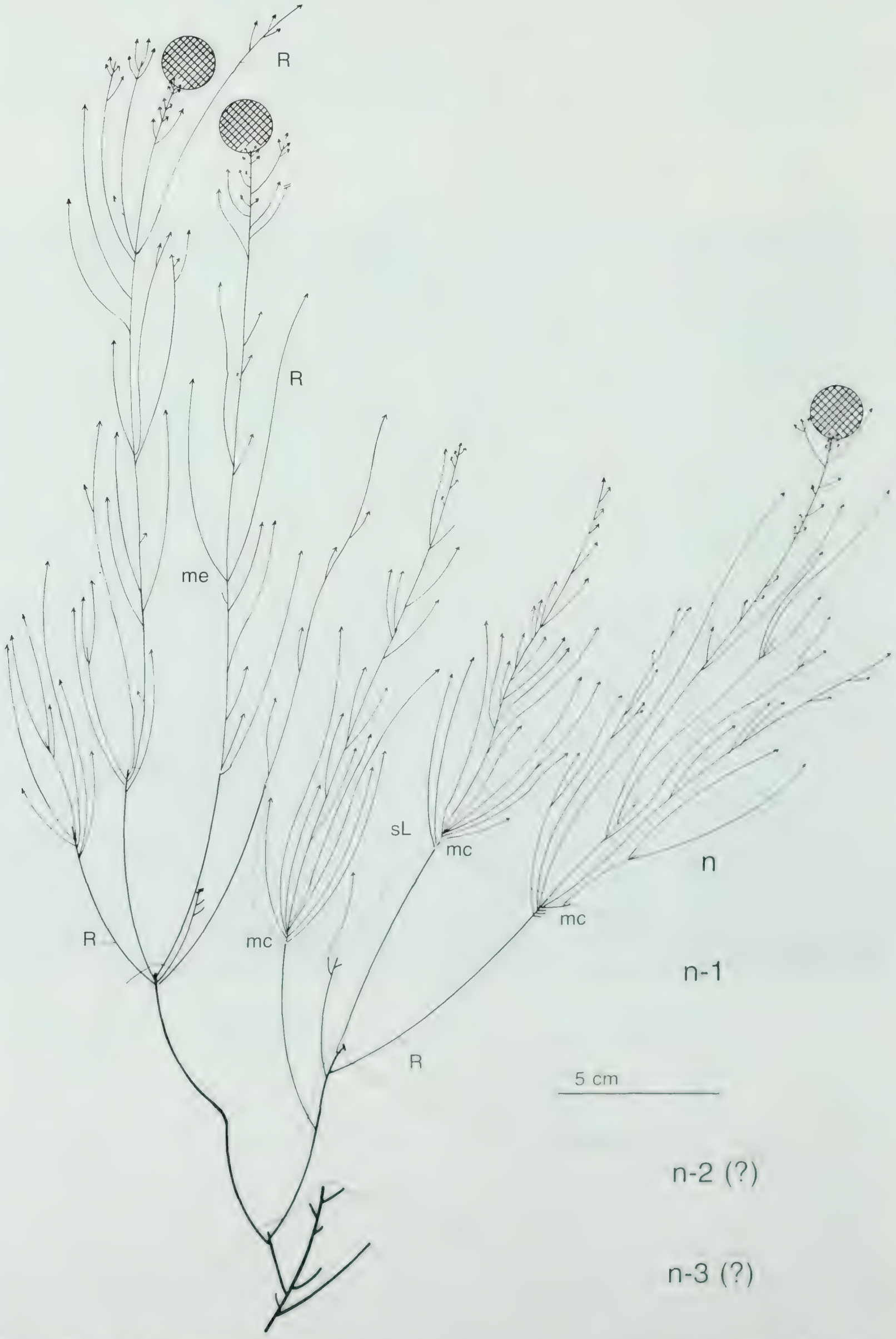


Figure 102 - **Nebelia fragarioides**. *Profile of a shoot system of a young plant showing the well developed vegetative branch system and the first terminal inflorescence aggregates.* sL, *sylleptic lateral shoot.*

The shoot system shown in fig. 104 illustrates a life stage which is intermediate between the early (fig. 102,103) and late flowering stage (fig. 105). While the flowering shoot of season n-4 is much-branched as are the younger flowering shoots (fig. 102,103), the flowering shoots of the seasons n-3 and n lack any vegetative lateral shoots and, thus, any chance of renewal.

The tendency to differentiate between solely vegetative and solely reproductive SGUs increases in older plants. In fig. 105 a flowering shoot system of an approximately fifteen year old plant is shown. The characteristic attribute of this stage is the paucity of sylleptic vegetative lateral shoots and the tiered arrangement of the inflorescences. The flowering shoots are unbranched, relatively short and lack renewal capacity. After fruit set they die and fall off. The shoot system is continued by means of unbranched renewal shoots which do not flower but produce both the primordia for the next season´s flowering and renewal shoots below the apex. The latter more or less dies off at the end of the season. The overtopping of the deflorated flowering zones by the actual inflorescences is therefore the result of a sympodial branching pattern and marked shoot dimorphism. The vegetative shoots not only function as renewal shoots but also as "carriers" of the next season´s inflorescences.

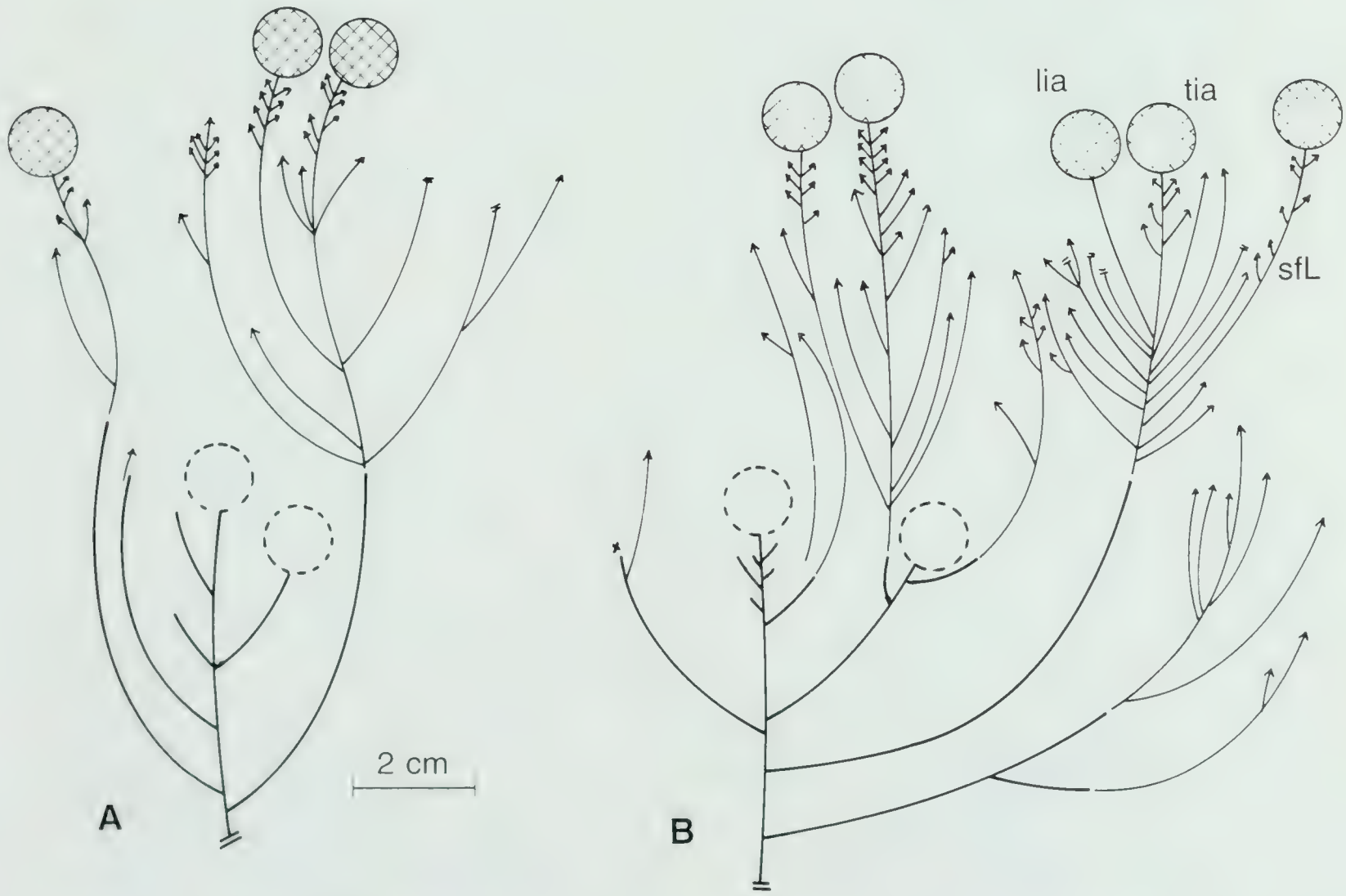


Figure 103 - **Nebelia fragarioides**. *A,B, profiles of shoot systems of young plants. Note the extensive branching below the terminal inflorescence aggregates and the presence of sylleptic lateral flowering shoots.*

N. stokoei (fig. 106, 107B) has compound inflorescences similar to those of *N. fragarioides*. However, the inhibition zone below the inflorescence is not as marked, with only the lowest lateral inflorescences being retarded in their development (fig. 106B). The flowering shoot system illustrated in fig. 106A presumably comes from a young shrub. In contrast to *N. fragarioides* the flowering shoots are largely sylleptically branched (svL´, sfL´). They are characterized by several lateral flowering shoots of 1st order (I) which may also be branched (svL´´, sfL´´) and occasionally have inflorescences of 2nd order (II). Within the flowering SGU a slight mesotony of the sylleptic lateral shoots is present. However, the renewal of the shoot system (R) arises from lateral shoots which develop cataleptically and immediately below the terminal inflorescence. As regards the SGUs, this species does not resemble *N. fragarioides* in having a distinct separation of function into flowering and renewal shoots.

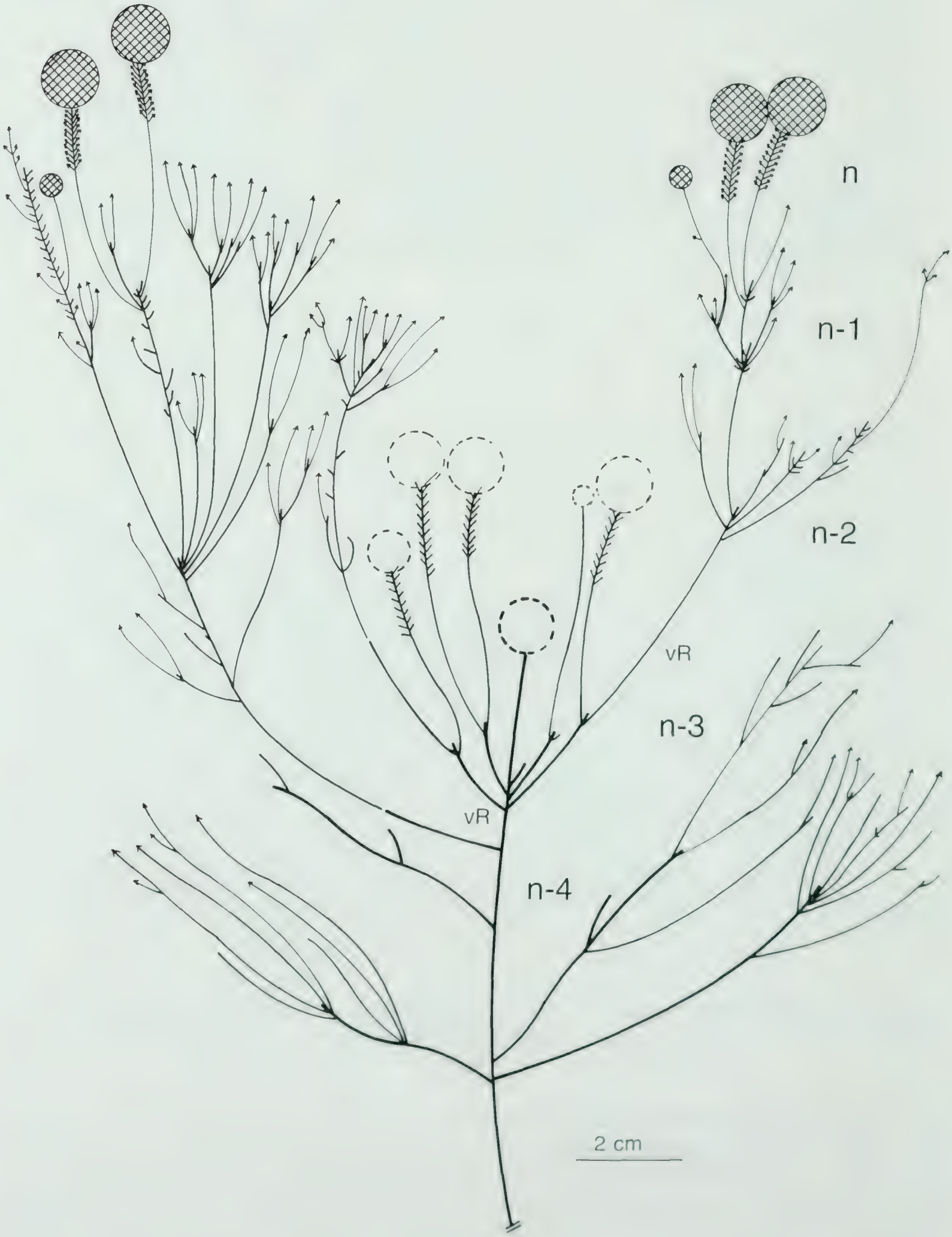


Figure 104 - **Nebelia fragarioides**. *Profile of a flowering shoot system of an adult plant. Note the increasing tendency for separation between flowering shoots and shoots for vegetative renewal only*

vR, *vegetative renewal shoot*

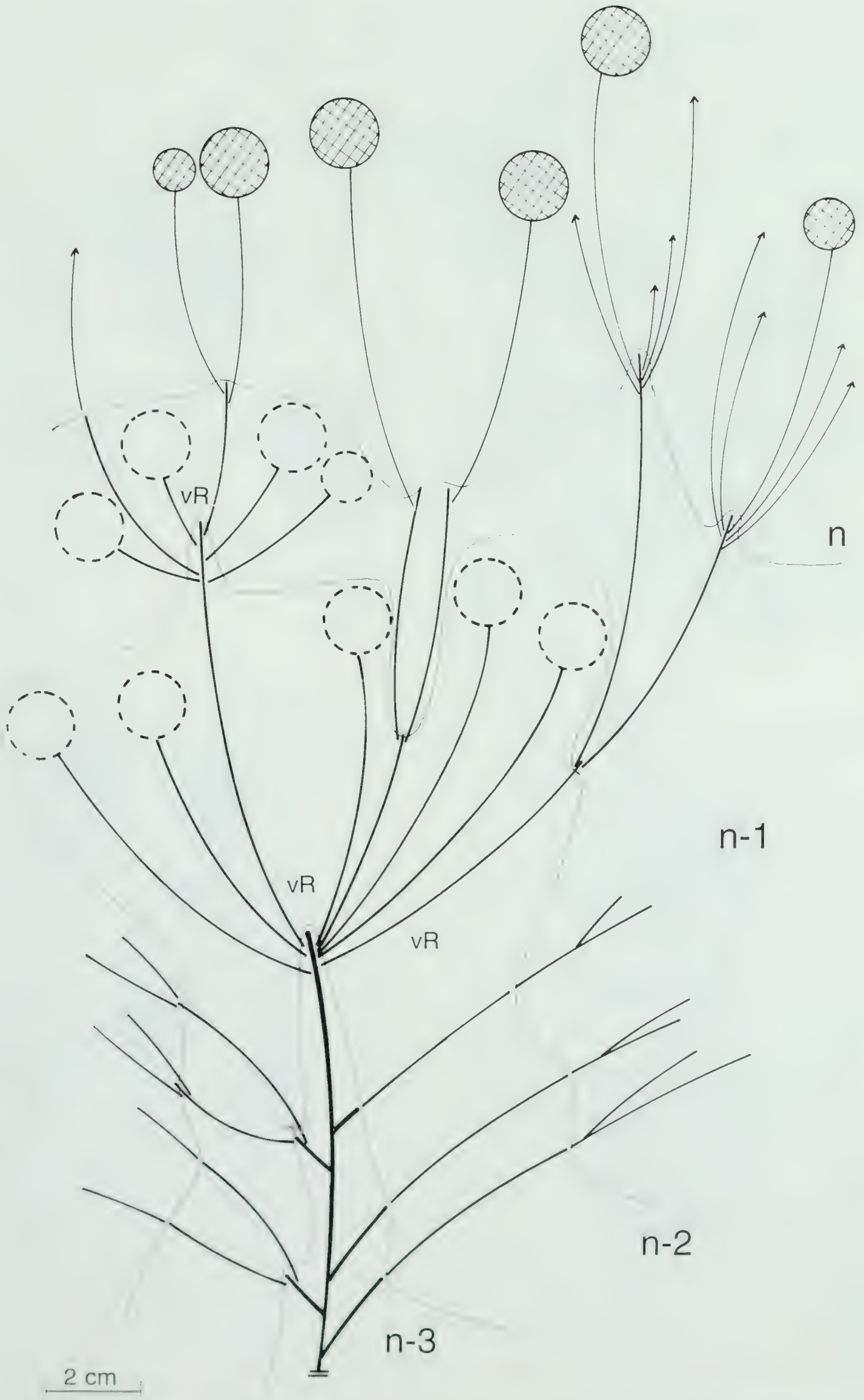


Figure 105 - **Nebelia fragarioides**. *Profile of a flowering shoot system of an old plant showing the arrangement of the inflorescence aggregates in tiers and the clear dimorphism between vegetative and reproductive shoots.*

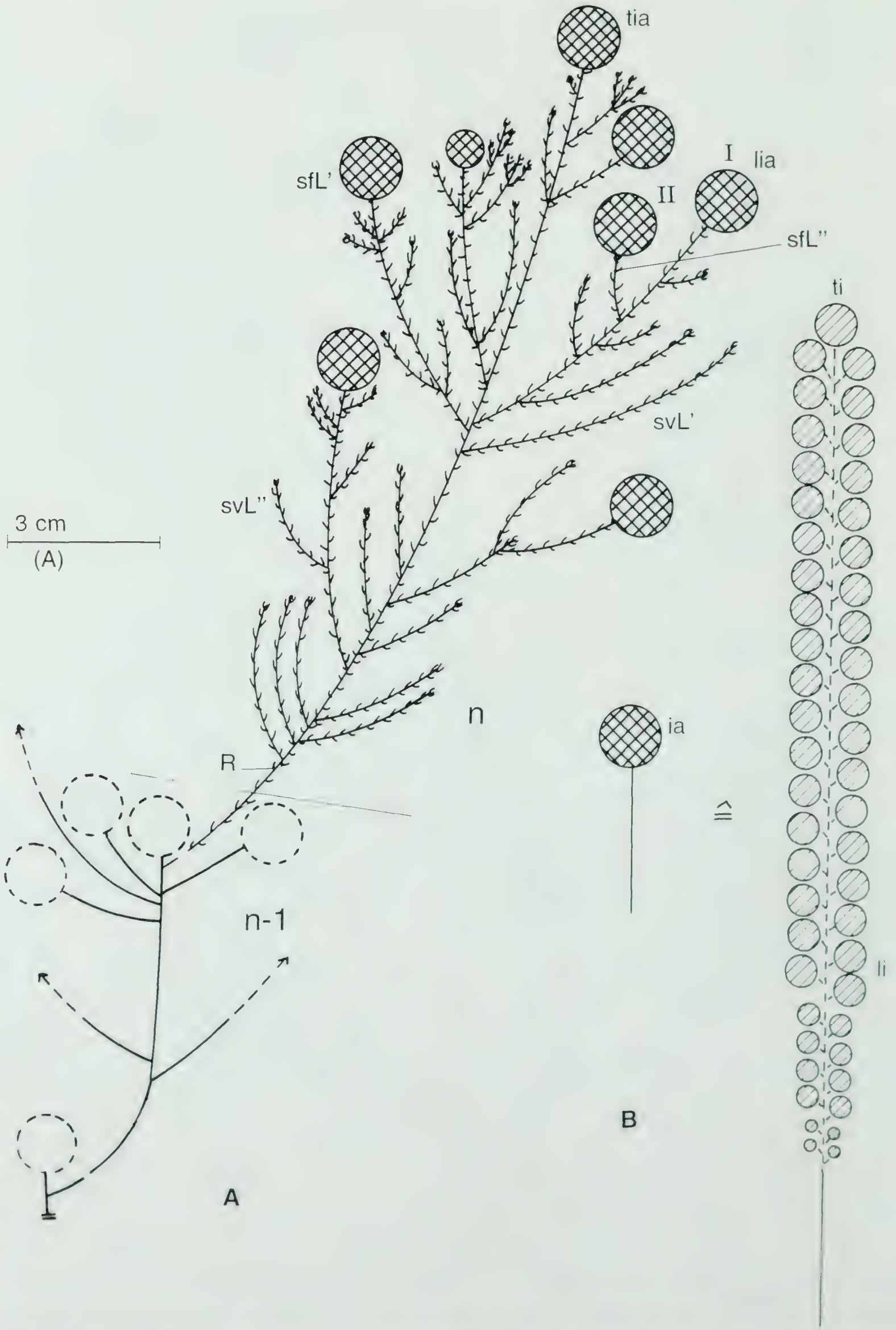


Figure 106 - **Nebelia stokoei**. *A, profile of a flowering shoot system, B, profile of the inflorescence aggregate showing its compound nature and the increasing inhibition of lateral inflorescences at its base*

ia, *aggregate of inflorescences*

Figure 107 - **Nebelia**. *A*, N. fragarioides, *seedling, three seasons old (compare with fig. 101A; Claßen & Froebe 1412, CLA), B*, N. stokoei *(Esterhuysen 33362, BOL), C*, N. sphaerocephala *(Esterhuysen 9671, NBG), D*, N. laevis *(M.R.L. 5467, BOL).*

The remaining species of the genus *Nebelia* lack compound inflorescences. *N. sphaerocephala* (fig. 107C) differs from *N. laevis* and *N. paleacea* in always having terminal inflorescences, while the other two species bear lateral inflorescences only (fig. 107D).

The SGU of *N. sphaerocephala* is subdivided into a proximal vegetative zone and a distal flowering zone which comprises the terminal and three to six lateral inflorescences (fig. 108,109: ti, sfL). The lateral flowering shoots are always unbranched and lack renewal capacity. Thus, there is a dimorphic shoot system present which comprises the flowering main axis and the sylleptic flowering lateral branches. The shoot system is renewed by vegetative shoots which either arise from the flowering zone (fig. 108, 109: svL) or, because of a marked mesotony (fig. 108, 109A: me), from the medial part of the SGU (fig. 109A: R). A clear renewal zone below the terminal inflorescence is absent. The branching pattern is regularly sympodial. However, as the prospective renewal shoots grow out syllepticaly and continue to grow and to flower during the following season, two seasons are involved in forming one SGU.

N. laevis (fig. 107D) and *N. paleacea* very rarely have terminal inflorescences. Usually the individual SGU is characterized by a distal flowering zone and an apex which grows on in the next season (fig. 110, 111: sfL, mc).

The characteristic pattern of flowering shoots in *N. laevis* shown in figure 110 and figure 111 is the result of repeated monopodial shoot connections combined with relatively short SGUs. The latter largely lack lateral vegetative shoots but bear dense clusters of inflorescences. Occasionally sylleptic vegetative lateral shoots appear. They either continue to grow on for several seasons (fig. 111B: svL) or flower cataleptically (fig. 110A, 111B: cfL). As in *N. sphaerocephala*, the lateral flowering shoots in *N. laevis* are usually unbranched short-shoots ending in an inflorescence of 1st order. Only very rarely do inflorescences of 2nd order appear (fig. 110B: II). Besides the monopodial connection of individual SGUs, the shoot system is renewed by lateral renewal shoots (R) which arise below (fig. 110B) or among the flowering shoots (fig. 111A). Occasionally vegetative shoots from an older part of the shoot system (which have grown on for several seasons) may function as additional renewal shoots (fig. 110A, n-2: svL, R). In the rare case of a terminal inflorescence, the renewal shoots arise immediately below the terminal inflorescence (fig. 110A, 111A,B: ti).

N. paleacea is quite common in the South Western Cape Province. The shrubs attain a height of about one meter. They are much-branched and bear numerous attractive inflorescences (fig. 112A,B). As in the case of *N.laevis*, the flowering zones are arranged in tiers, either because of repeated monopodial connections (fig. 113B) or because of overtopping by lateral renewal shoots (fig. 113A).

Figure 114 shows the profile of a shoot system representing five seasons growth. After three seasons of vegetative growth (n-4 - n-2), the growth increments being connected in a monopodial manner (mc), the shoot system commences flowering (n-1,n). The arrangement of the inflorescences is more variable than in *N. laevis*. The distal part of the flowering zone is characterized by unbranched lateral flowering shoots, the middle part by determinate lateral shoots (dL´) with inflorescences of 1st (I) and 2nd order (II), and the basal part by indeterminate lateral shoots (iL´). The latter have inflorescences of 2nd order (II) or indeterminate lateral shoots (iL´´) which consequently bear inflorescences of 3rd order (III).

In contrast to *N. laevis* vegetative shoots are largely lacking within the flowering SGUs. Thus, when the apex dies off, the shoot system depends for renewal on vegetative shoots from a preceding season. As is illustrated in fig. 114, the deflorated flowering zone of season n-1 is overtopped by flowering shoots (n) which have started to grow out as sylleptic vegetative lateral shoots in season n-2, in doing so showing a marked mesotony (me).

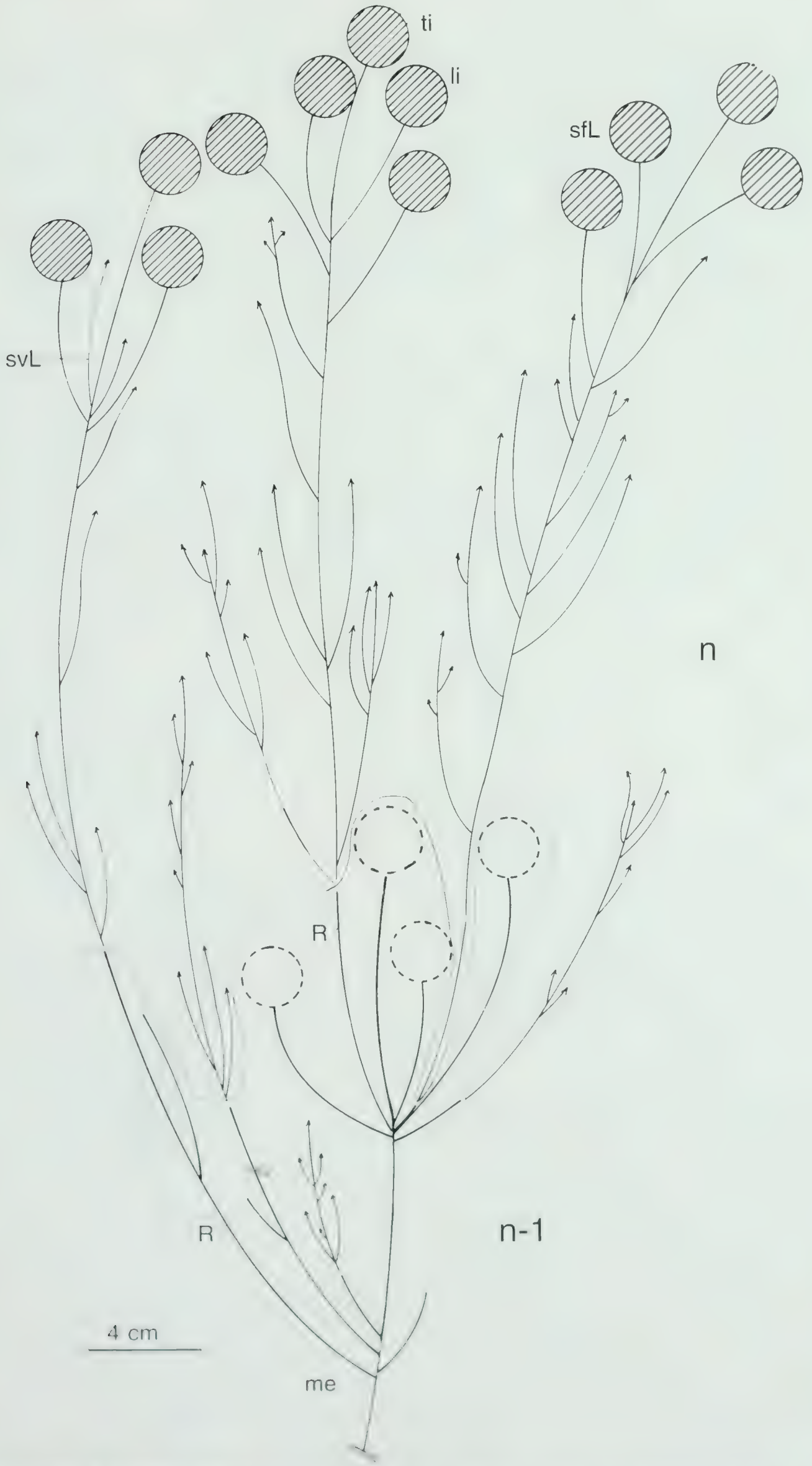


Figure 108 - **Nebelia sphaerocephala**. *Profile of a flowering shoot system, two seasons old. Note the presence of a terminal inflorescence, the unbranched lateral flowering shoots, the marked mesotony and the variable position of the renewal shoots*

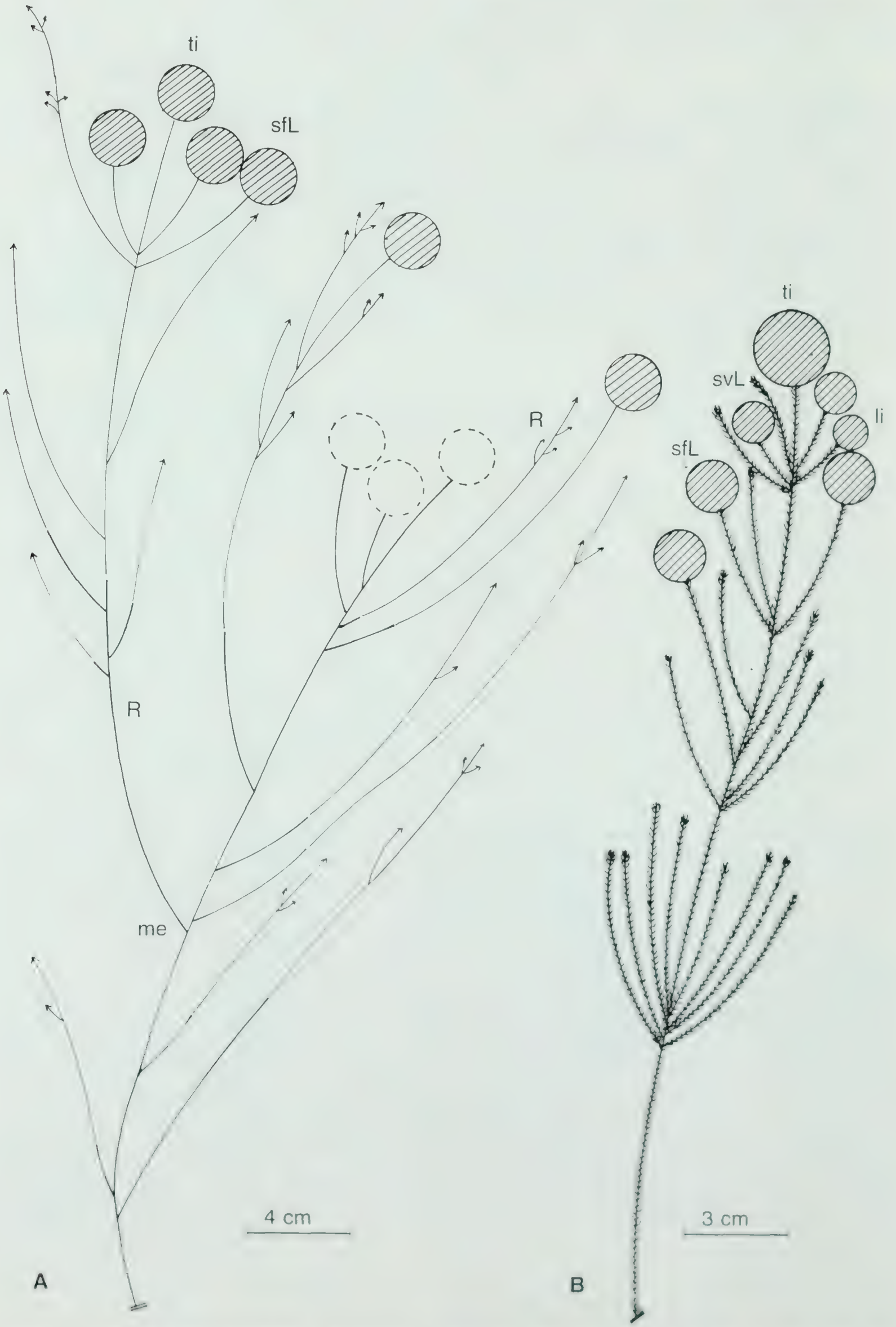


Figure 109 - **Nebelia sphaerocephala**. *A,B, profiles of flowering shoots systems, in B with foliage. Note the presence of a terminal inflorescence, the unbranched lateral flowering shoots, the marked mesotony and the variable position of the renewal shoots.*

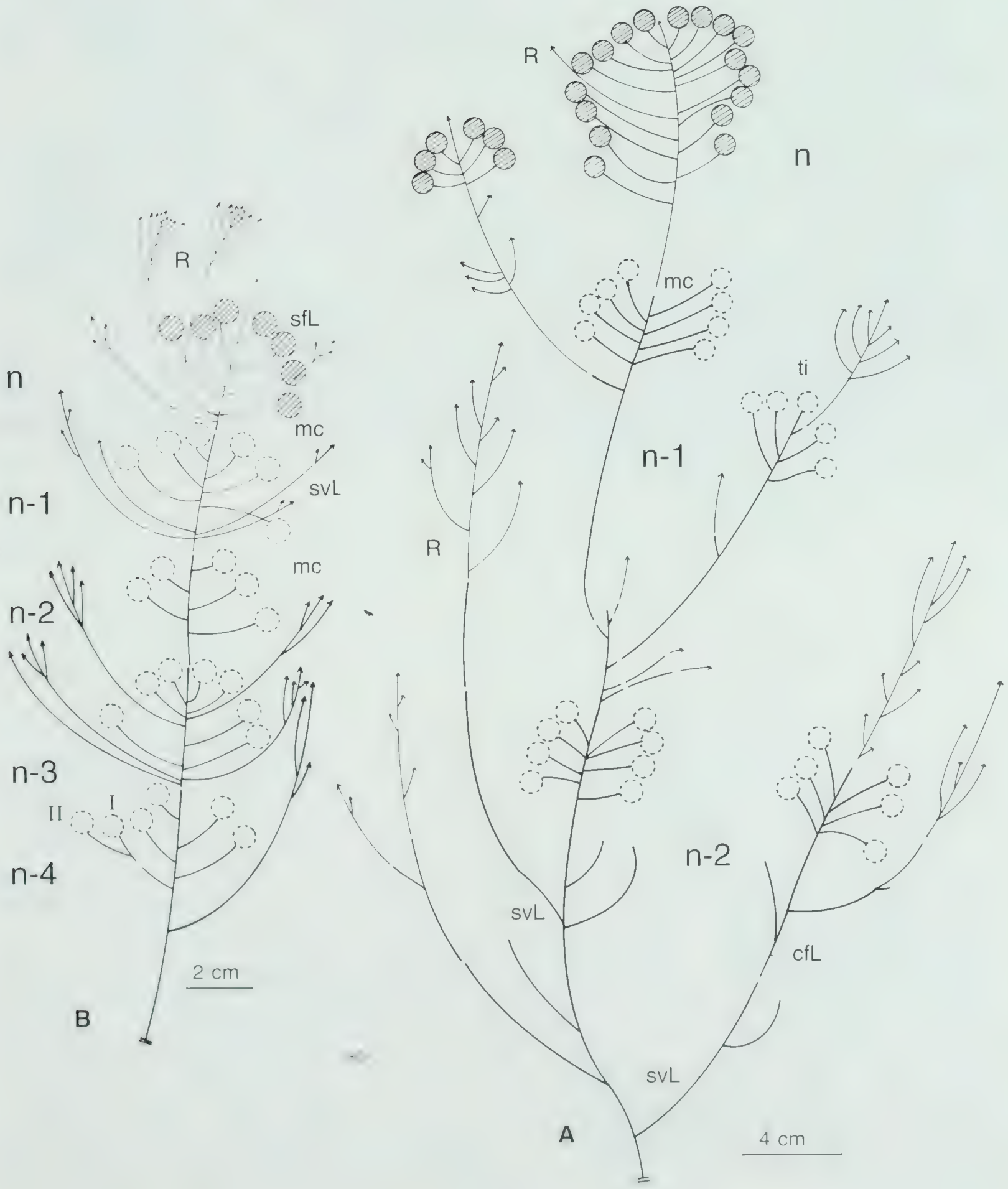


Figure 110 - **Nebelia laevis**. *A,B, profiles of flowering shoot systems, three (A) and five (B) seasons old. Note the paucity of terminal inflorescences, the numerous monopodial connections and the characteristic arrangement of the flowering zones in tiers.*

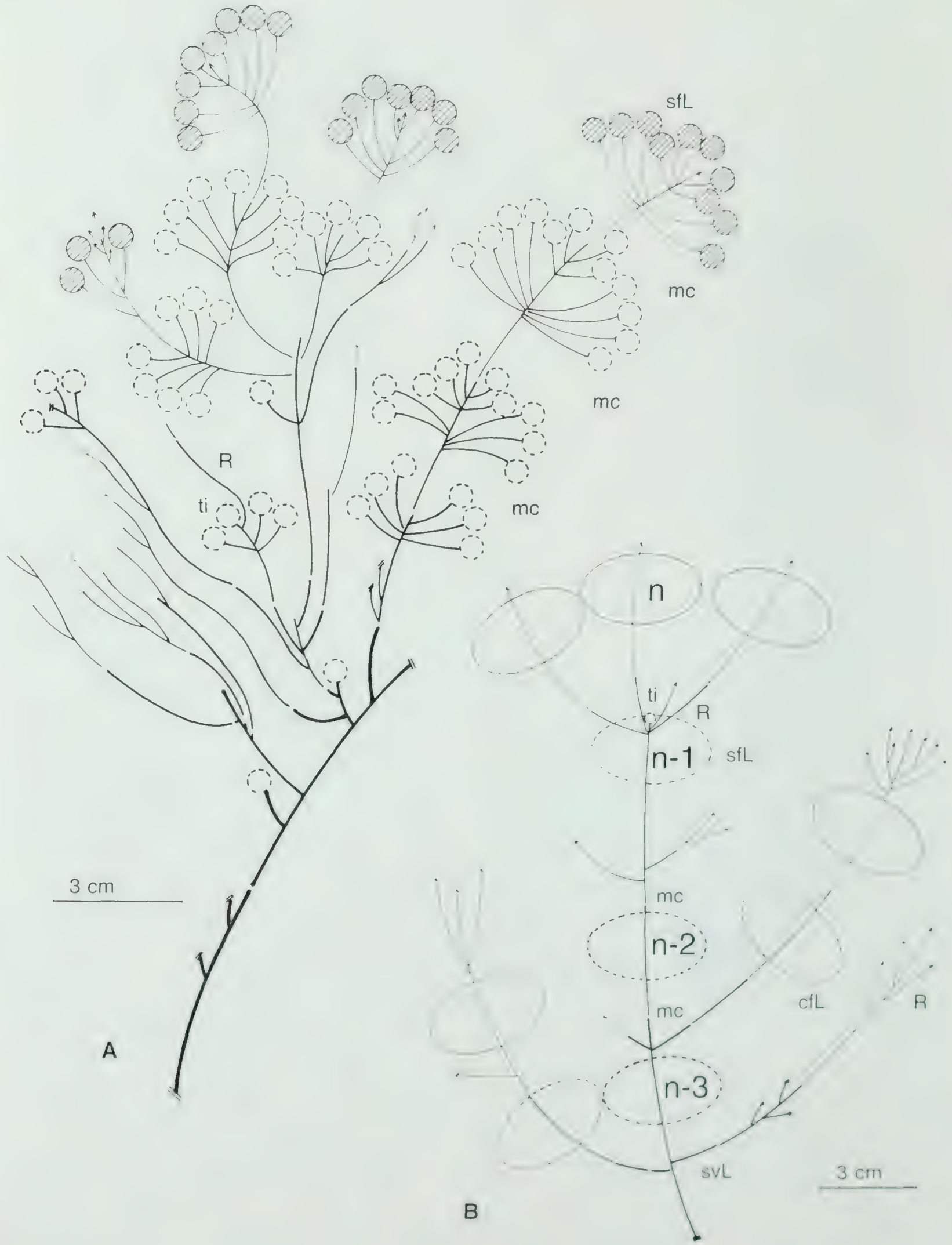


Figure 111 - **Nebelia laevis**. *A,B, profiles of flowering shoot systems, in B flowering zones only outlined. Note the complete lack of vegetative shoots in the flowering SGUs in A, the very rare presence of a terminal inflorescence and the numerous monopodial connections within an individual sympodial unit.*

Figure 112 - **Nebelia paleacea**. *Flowering shrubs at Landrostkop (A) and at Vogelgat Nature Reserve (B) (compare with figure 113B).*

Figure 115A shows a selected part of the flowering shoot system of an older shrub. Greater age is evidenced by the presence of very short SGUs which very often are connected in a monopodial manner (mc). The flowering shoots are all unbranched, terminating in an inflorescence of 1st order. Occasionally a terminal inflorescence (ti) appears, but inflorescences of 2nd order were not found.

Though the individual SGUs are short and relatively simply organized, they vary considerably. Besides the flowering SGUs, individual solely vegetative SGUs may be present. As the summary scheme in fig. 115B illustrates, the apex terminates in an inflorescence (I), dies off (II) or continues to grow on in the next season (III-V). Up to four monopodial connections are possible (compare with fig. 113B) before the apex dies off or flowers. The shoot system must then be renewed sympodially by lateral shoots, which appear either below the terminal inflorescence (I) or below the vegetative apex (II, III) and/or among (V) or below the flowering shoots (I,II,IV,V).

The remarkable differences between the two profiles of *N. paleacea* shown in fig. 114 and in fig. 115 are presumably related to different age classes. The younger shoot system (fig. 114) shows the characteristic high vegetative vitality of shrubs which are able to rejuvenate after fire. It may pass into the pattern of the older shoot system (fig. 115A) by reduction of the individual SGUs and by repeated monopodial connections. That the flowering zone illustrated in fig. 114 (n-1) does not in fact grow on, may be due to external influences, e.g. browser damage.

Leaf metamorphosis and inflorescence structure. The inflorescences of *Nebelia* species are either arranged solitarily *(N. sphaerocephala, N. laevis, N. paleacea)* or in spherical aggregates formed by 30-50 (*N. fragarioides*, fig. 101B) or 20-30 (*N. stokoei*, fig. 106B) individual inflorescences. Whatever the organization of the inflorescences, all are relatively large (1-2 cm in diameter), conspicuous pincushion-like structures.

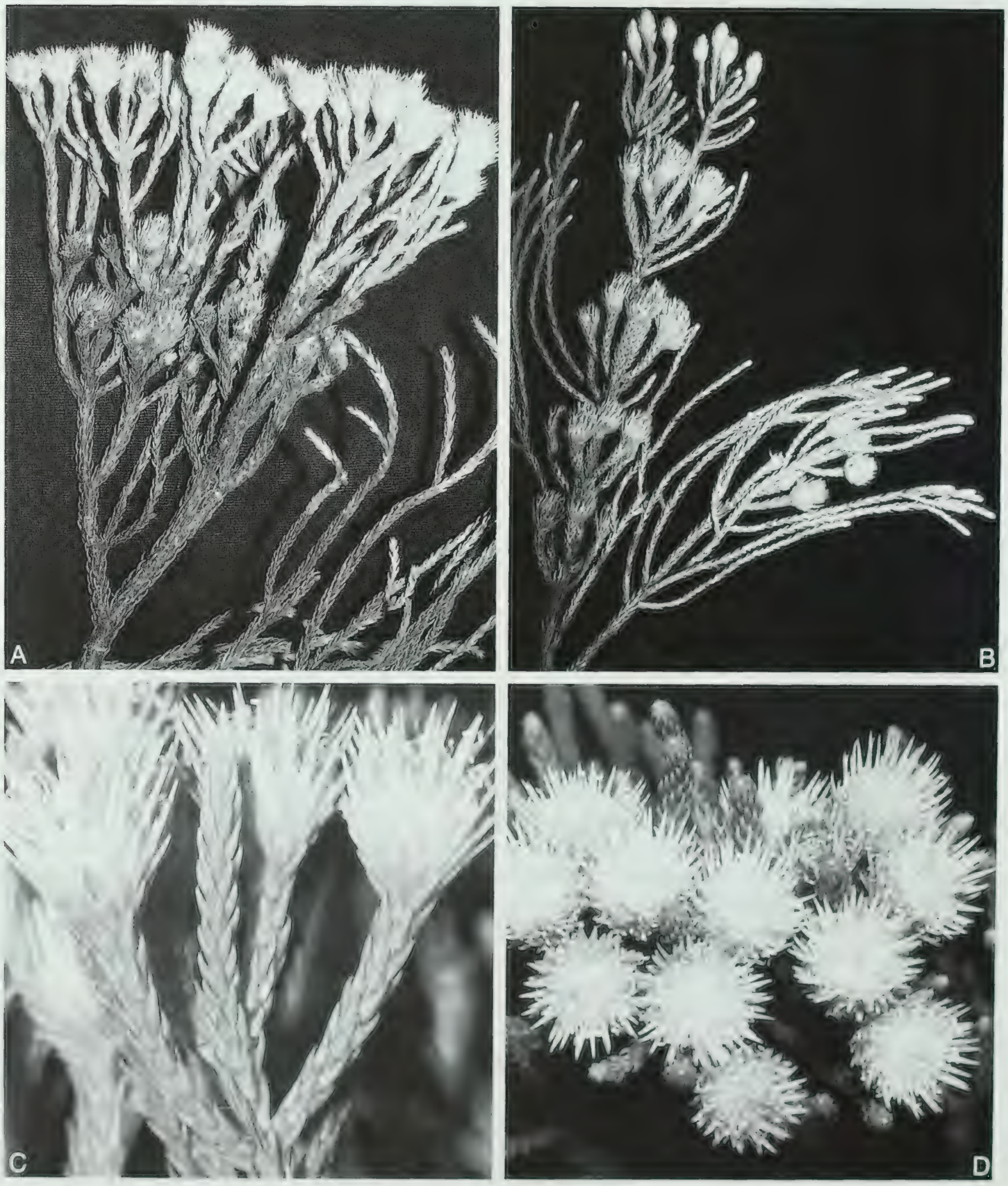


Figure 113 - **Nebelia paleacea**. *A,B, flowering shoot systems from a locality above Hermanus (A) and from a locality at Vogelgat Nature Reserve (B; compare with fig. 112B). Note the characteristic arrangement of the inflorescences in tiers. C, detail from A, showing the lateral arrangement of unbranched flowering shoots round the main axis, which remains capable of growing on in the next season. D, a flowering zone from above showing the attractive inflorescences. Note the conspicuous cream-coloured involucral bracts in C and D*

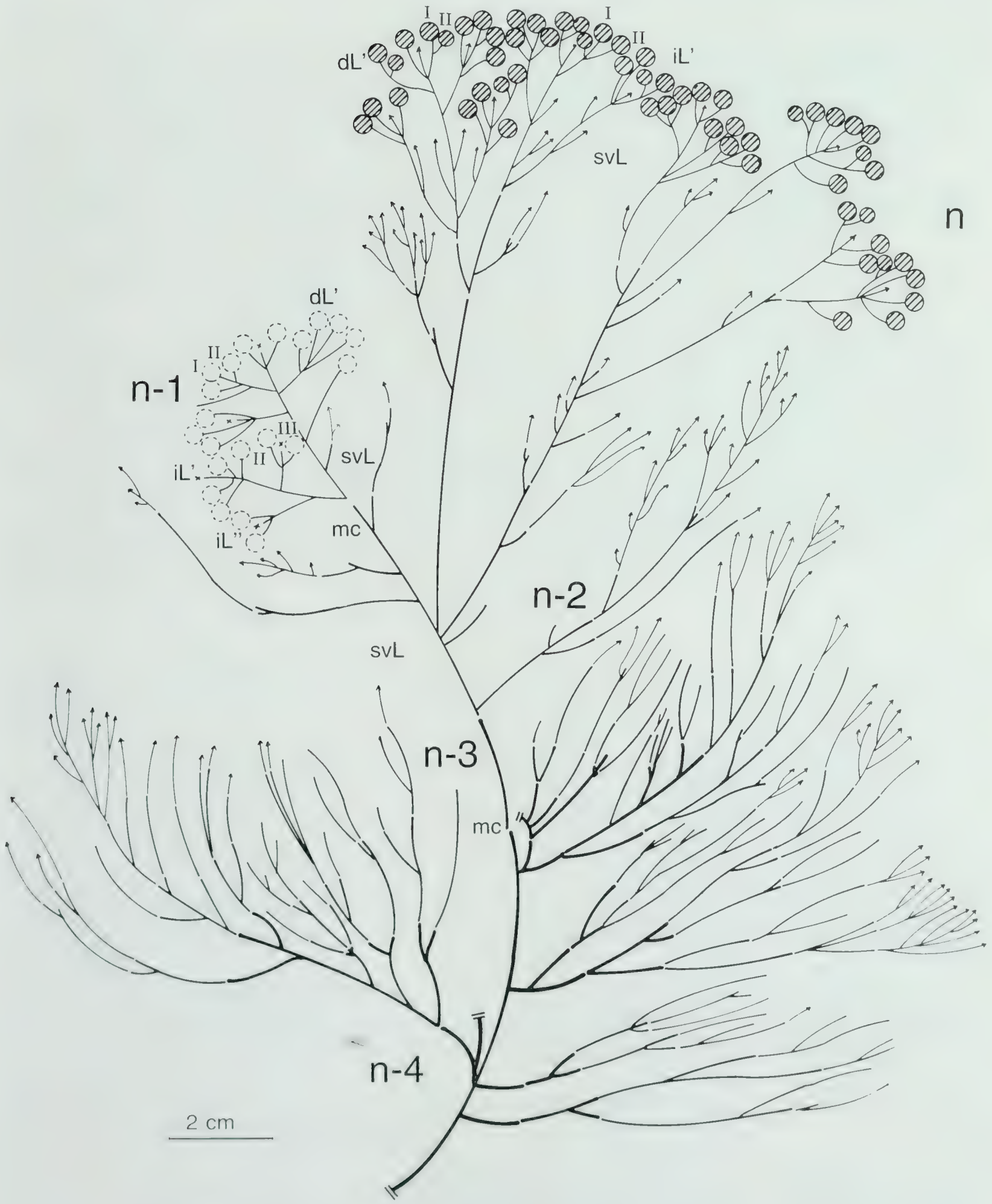


Figure 114 - **Nebelia palcacca**. *Profile of a five-season old shoot system rejuvenated after fire. Note the rich vegetative branching in the basal zone and renewal from mesotonic shoots of season n-2.*

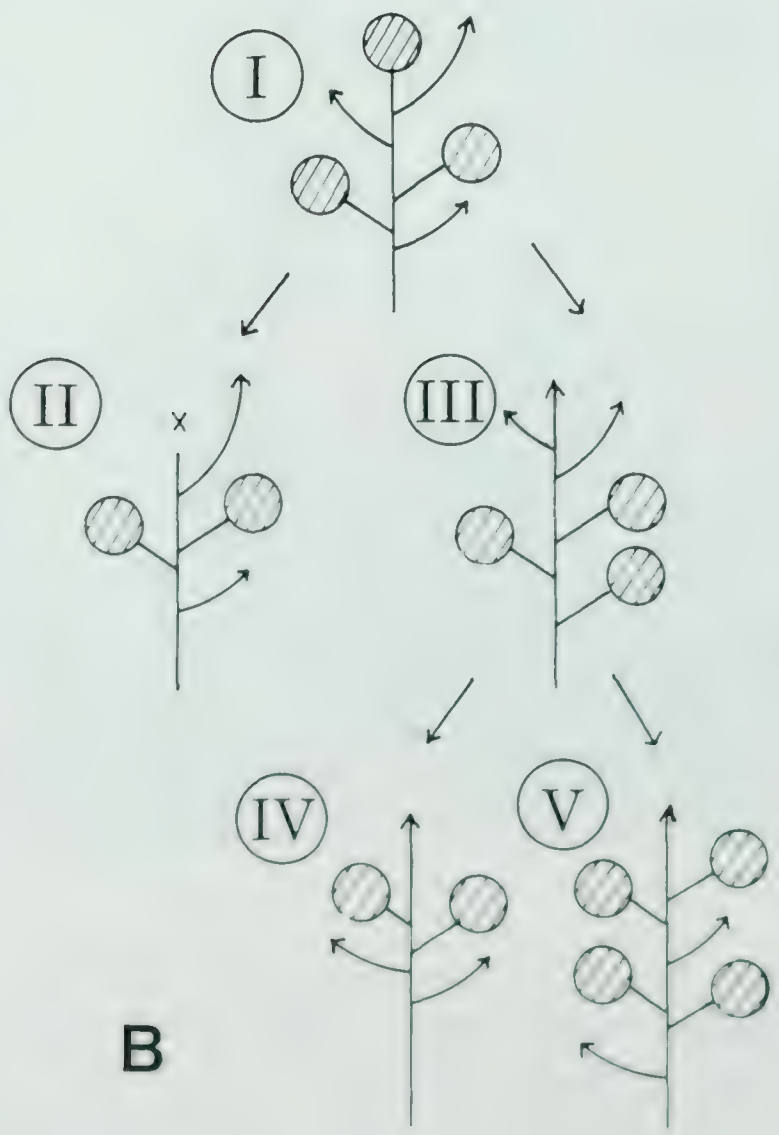


Figure 115 - **Nebelia paleacea**. *A, profile of a flowering shoot system, five seasons old. B, variability of the SGUs.*
I-V *in B correspond to* I-V *in A*

The compound nature of the inflorescences in *N. fragarioides* and *N. stokoei* is visible only in the prefloral stage, when individual inflorescences still are separated from each other by their involucres (fig. 100A). When the plants are in flower, the numerous exserted stamens mask the compound nature of the inflorescence, transforming the whole cluster of inflorescences into a pincushion-blossom (fig. 100B).

The compound inflorescences of the two species mentioned above resemble the simple one of *N. sphaerocephala.* Fig. 116 shows that the "pincushions" are not only of the same size (A,D,E), but have a similar thick receptacle (A´´,D,E) which bears up to one hundred, exclusively lateral flowers (*N. sphaerocephala)* or a terminal and several lateral inflorescences, each with five or ten florets only, in the two species with compound inflorescences (*N. fragarioides, N. stokoei*).

Each flower has a subtending bract and two prophylls. It is presumed that the individual inflorescence is indeterminate, because no terminal flower has been found in any species and because the uppermost flowers often are inhibited. However, a clear evidence of sterile apex is lacking.

Within those *Nebelia* species which bear simple inflorescences, there appears to be a tendency to form inflorescence blossoms (fig. 116A-C). In a developmental series *N. sphaerocephala* → *N. laevis* → *N. paleacea,* the inflorescence axis becomes progressively shorter and flatter, the number of florets per inflorescence decreases and the number of sterile involucral bracts increases. The end-product is the bowl-shaped inflorescence of *N. paleacea* characterized by the presence of numerous cream-coloured involucral bracts (fig. 113C,D).

Although prominent involucral bracts may function in pollinator attraction, the absolute length of the involucral bracts (see fig. 116) does not necessarily signal greater pollinator appeal. Especially in *N. sphaerocephala* and in *N. laevis,* the involucral bracts are extremely curved and probably function more as protective than attractive organs. As a general tendency all involucral bracts have ciliate creamish leaf margins (fig. 116A´-E´), but only in *N. paleacea* does the entire leaf blade become creamish-white (fig. 116C´).

Summary. The five species analysed all exhibit high vegetative vitality and appear capable of forming rejuvenative shoots at all life stages. This may be the product of a very short vegetative life stage with flowering beginning before the shoot system is fully developed.

The model in fig. 118 does not represent the branching and flowering pattern of a particular species but summarizes the characteristic features of the genus. In A the reference system (RS) of *Nebelia* is illustrated. The apex always remains open and dies off after having formed a terminal inflorescence (ti). The individual inflorescence is a truncate cephaloid. Below the inflorescence the subfloral renewal zone (rz) is present. The extended branching zone (bz) has sylleptic vegetative (svL) and flowering lateral shoots (sfL). Mesotonous vegetative shoots may function as additional renewal shoots (me). The flowering shoots are unbranched or branched and in the latter case either determinate (dL) or indeterminate (iL).

Despite the range of variability in the genus, three groups of species are distinguishable:

- *N. sphaerocephala:* simple inflorescences in a terminal and lateral position, sympodial shoot system;
- *N. stokoei, N. fragarioides:* compound inflorescences in a predominantly terminal position, sympodial shoot system,
- *N. laevis, N. paleacea:* simple inflorescences in a predominantly lateral position, sympodial shoot system with several monopodial inserts.

N. sphaerocephala (B) is very similar in construction to the basic model. However, the branching zone is more homogeneous having only unbranched lateral flowering shoots. The sympodial units are not strictly speaking formed within one season, because the renewal shoots grow out sylleptically, then become dormant and resume growth in the next season.

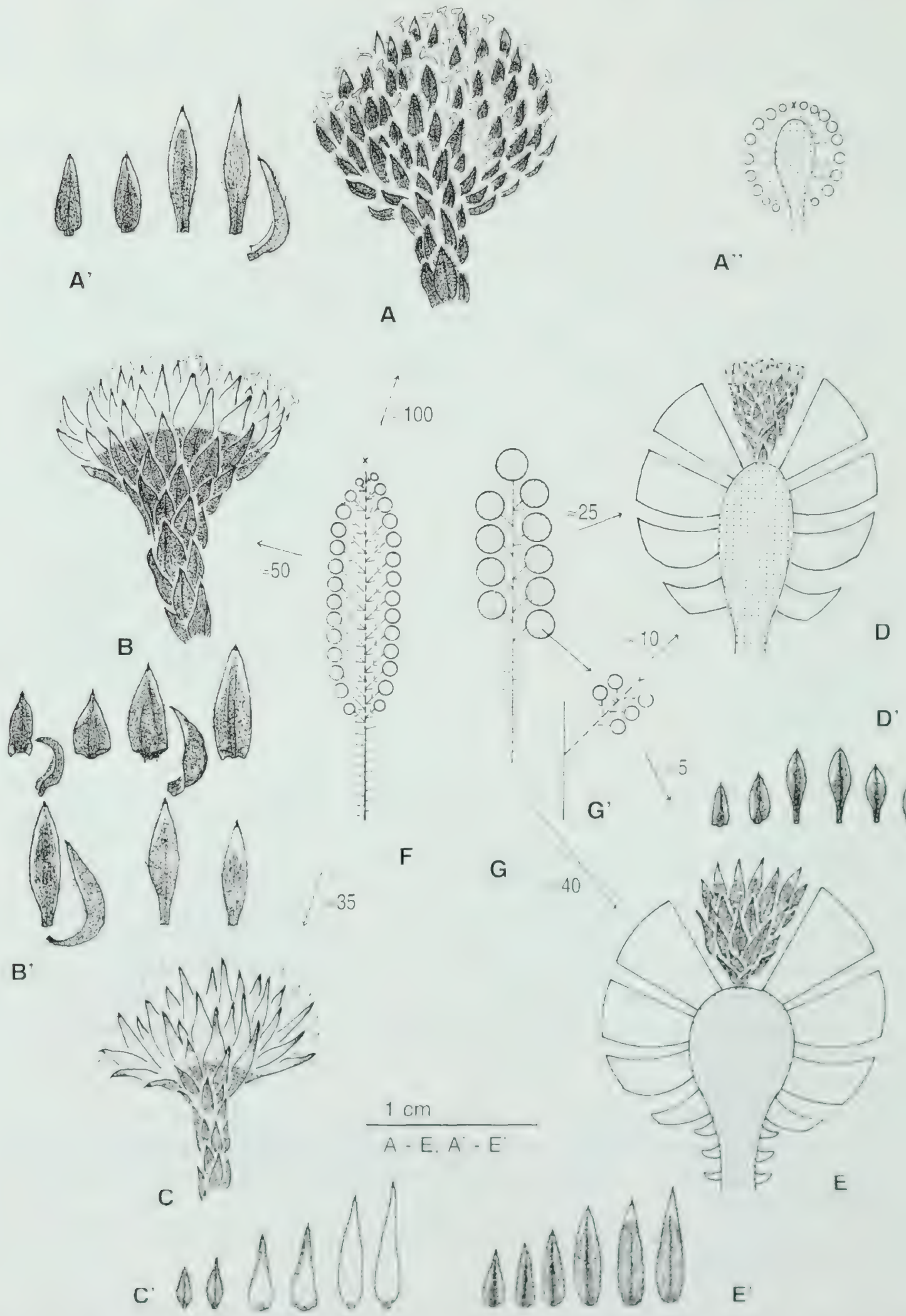


Figure 116 - **Nebelia***: Leaf metamorphosis and inflorescence structure. A-E, structure of the inflorescences, showing the compound nature in D and E; A'-E', leaf metamorphosis, showing (from left to right) the gradual transition from leaves to involucral bracts; A'', F-G', profile of the inflorescences, showing the organization of the simple and compound inflorescences and the average number of flowers per inflorescence and inflorescences per compound inflorescence. Note the analogous construction of the pincushion-blossoms in* N. sphaerocephala *(A, A'') and in* N. fragarioides *and* N. stokoei *(D,E) and the formation of attractive strawy involucral bracts in* N. paleacea. *A-A'',* N. sphaerocephala, *B,B',* N. laevis, *C,C'',* N. paleacea, *D,D',* N. stokoei, *E,E',* N. fragarioides.

N. stokoei and *N. fragarioides* (C) agree with the model as regards formation of the SGU within a single season. However, the inflorescences are compound (heterothetic double-heads). The renewal zone (rz) below the terminal individual inflorescence (ti) is entirely lacking, but appears below the terminal compound inflorescence (tia). It is not clear whether the original renewal zone has been displaced or whether a secondary renewal zone has been formed by mesotonous vegetative shoots. However the simple and the compound inflorescences of the genus *Nebelia* occupy similar position within the SGU and are thus homotopous (compare with § 4.3.3.2). Besides the different organization of the inflorescences, fully adult shrubs of *N. fragarioides* exhibit a tendency for physical separation of vegetative and reproductive SGUs (C′) (fig. 117). The general tendency of the genus to differentiate between vegetative and flowering shoots is thus repeated at a higher level of organization.

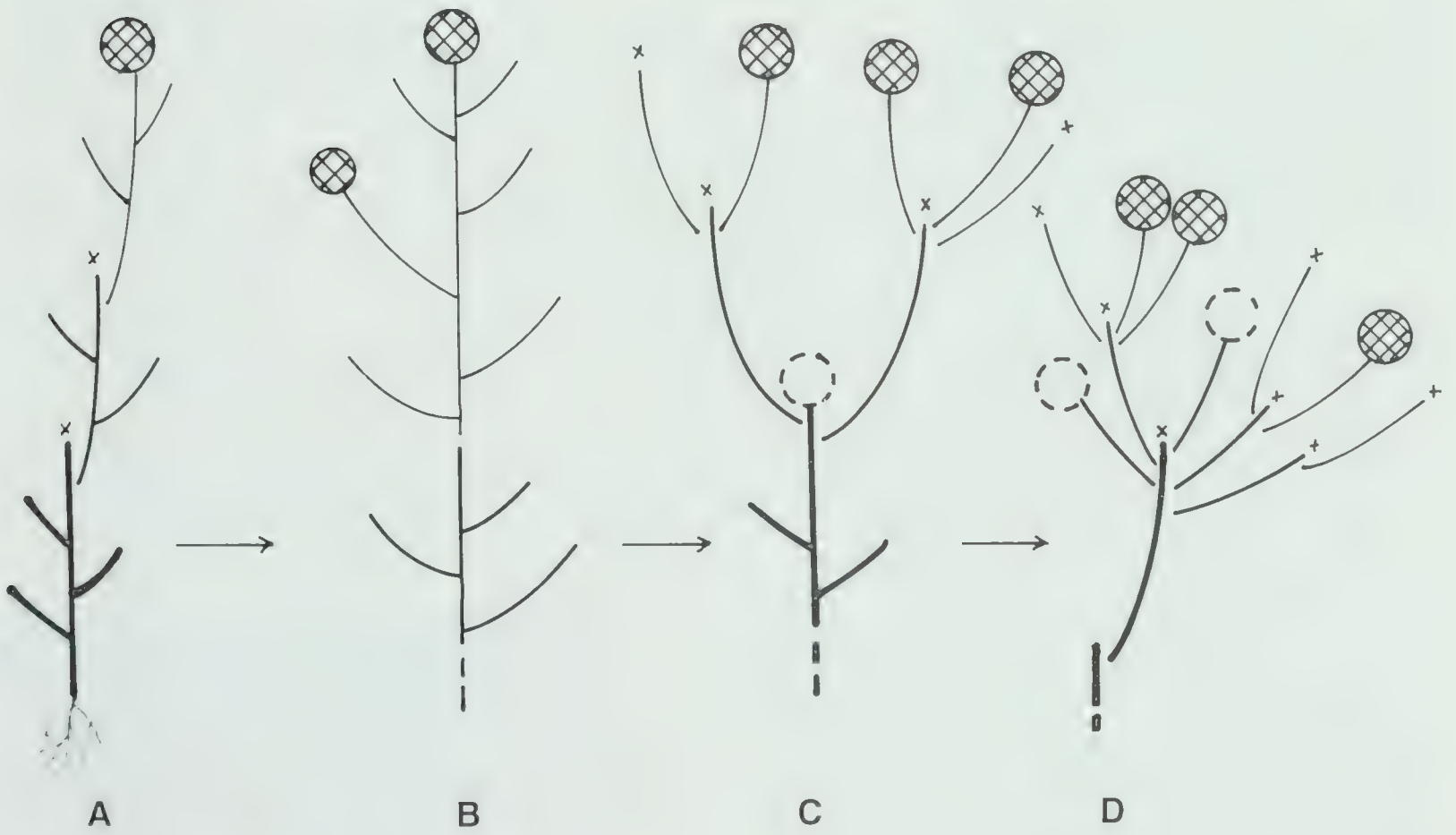


Figure 117 - ***Schematic life cycle of*** **Nebelia fragarioides.** *The first stage (A) is characterized by the presence of few vegetative SGUs, which are connected in a sympodial way. In the second stage (B) the shoots gain strength and are able to grow on for several seasons. The shoot system now fulfils multiple functions, developing an extensive vegetative system and flowering at the same time. Later on (C) the shoots gradually become shorter, show a decreased branching capacity and return to a sympodial branching pattern. Finally (D) the shoot system shows a clear sympodial connection of relatively short shoots and a separation into vegetative and reproductive SGUs.*

N. laevis and *N. paleacea* (D) show a further variation of the model. This concerns the behaviour of the apex, which is not constant in the two species mentioned. The apex very often remains open and active for several seasons, resulting in a monopodial shoot connection. In this case, the terminal inflorescence and the renewal zone are lacking. In reverting to a system of sympodial shoot connection, however, the renewal zone is present while the terminal inflorescence may be present or absent.

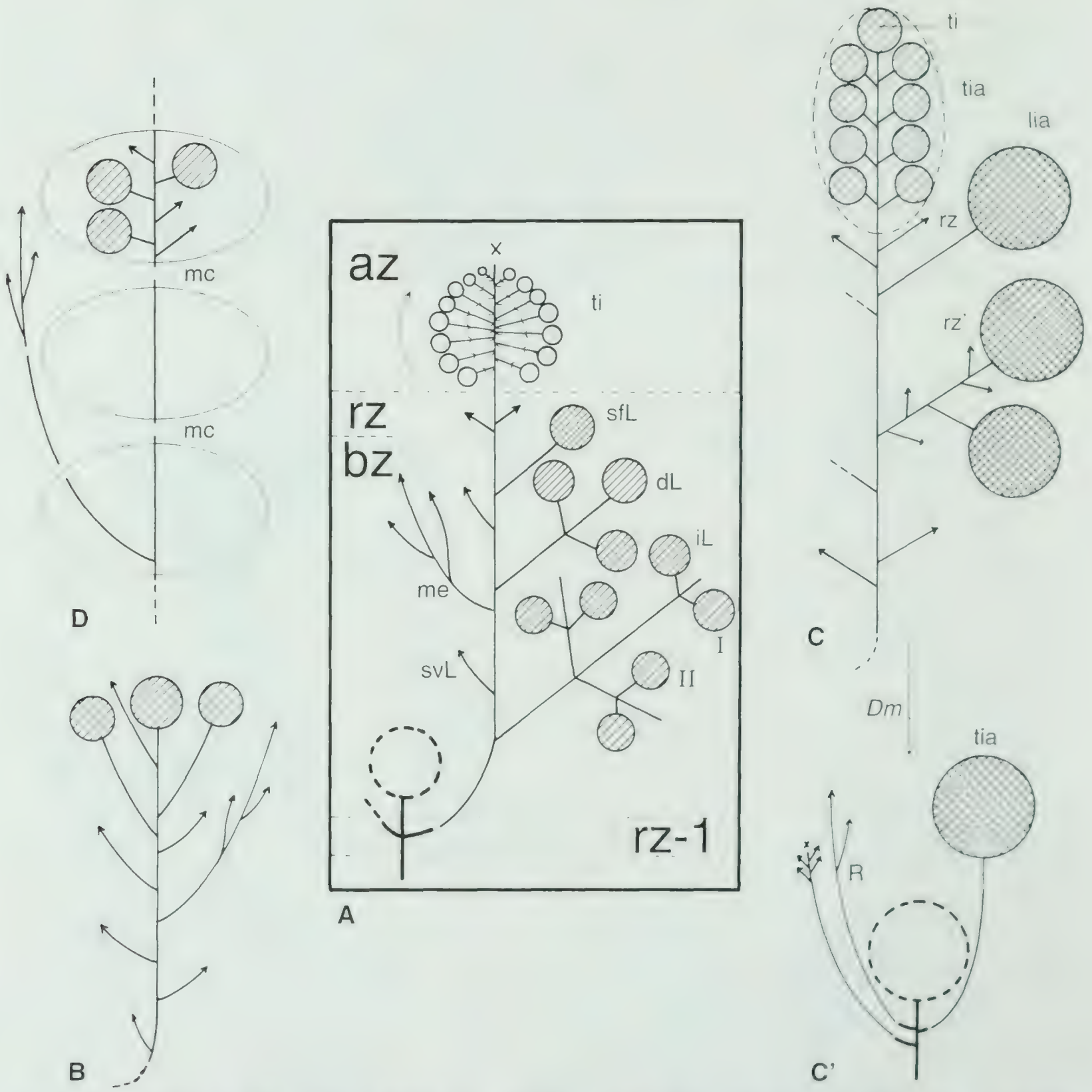


*Figure 118 - **Model of the genus** **Nebelia**. A, the RS of the genus showing an open apex, a terminal inflorescence, a subfloral renewal zone and a branching zone with many sylleptic vegetative and flowering lateral shoots. B-D, variation of the RS as regards the formation of compound inflorescences (C) and of shoot dimorphism (C'), the partial reduction of the branching zone (B) and the lack of a terminal inflorescence, giving rise to repeated monopodial shoot connections (D). Dm, dimorphism.*

3.8 *Pseudobaeckea* Niedenzu

The genus comprises four species. Two individuals of P. cordata *were studied at Jonkershoek Nature Reserve (2000-3000 ft), one of* P.teres *examined at the summit of Elandsberg (Ladismith) (7200 ft),* P. africana *was seen in cultivars at the nursery of the National Botanic Garden Kirstenbosch. Additional herbarium specimens of the three species mentioned were examined*

P. teres *differs from the other species of the genus in so many characters that it may be more appropriately placed in another genus (Pillans 1947:143, Carlquist 1991:31).*

Growth and branching pattern. The two specimens of *P. cordata* found at Jonkershoek (fig. 119A,B) were approximately one meter in height and one and a half meter in diameter. The species is extremely floriferous and showy when in full flower.

Fig. 120A, 121 and 122 show the habit and the profile of a two season old flowering shoot system. Its most conspicuous feature is an extensive sylleptically branched system which involves the entire dominant shoot but is most prominent at the base of the SGU concerned. In fig. 121 the actual SGU (n) begins with fifteen densely aggregated lateral shoots which are sylleptically branched in their mesotonous-distal zone, repeating the branching pattern of parent axis (fig. 122: C). As the shoots terminate in an inflorescence, a panicle-like arrangement of the SGU results (fig. 120A).

The false whorl of proximal lateral shoots is more or less separated from the medial and distal lateral shoots of the SGU, which are likewise aggregated but in more loose groups (fig. 120A, 121). The lateral shoots become shorter and less branched towards the proximal zone of the SGU. The distal zone bears only undeveloped lateral primordia and is characteristically curved. Presumably the apex continues to grow on in the next season, connecting the two SGUs monopodially in the same manner as the previous season (fig. 121, 122: mc).

Figure 119 - **Pseudobaeckea cordata**. *Shrubs in the Jonkershoek Nature Reserve, A, among dense vegetation beside a streamlet, B, on a rocky ledge.*

The entire shoot system is clothed with small globose inflorescences (fig. 120A,B). Fig. 122C demonstrates the arrangement of the inflorescences on a lateral shoot. Below the terminal inflorescence (I) lateral flowering shoots are present. These, from distal to proximal, are first sessile (II) and then shortly petiolate. The latter are further branched and bear additional inflorescences of 3rd order (III). The length of the lateral flowering shoots increases from top to base of the flowering zone, giving it a pyramidal appearance. Depending on the degree of aggregation, clearly separated aggregates of inflorescences (ia) are formed. These are illustrated in fig. 121 (ia), for the whole shoot system analyzed. The well developed proximal and medial lateral shoots may be subdivided into a terminal (tia´) and several lateral aggregates of inflorescences (lia´) while the shorter lateral shoots have only a single aggregate of inflorescences (ia) or even only one lateral, sessile inflorescence. The aggregates are not homogeneous as they are e.g. in *Berzelia*, but composed of inflorescences of different orders of branching (fig. 121,122, 124A).

The formation of aggregates is the result of small size and dense arrangement of the individual inflorescences; this is emphasised by the separation of one aggregate from another by extended leafy shoots (fig. 121, 122). Within individual aggregates sterile leaves are also present (fig. 122, 124A). These do not contribute to the general appearance of the inflorescence, but are important as regards to the structure of the shoot system as since it is below the terminal individual inflorescence that renewal shoots are formed (fig. 122E, 124A: rz, R).

As shown in fig. 120B and 123 both types of shoot connection, monopodial (A) and sympodial (B), may be present within an individual shoot system. Only the dominant renewal shoot remains open and continues to grow on in the next season; the remainder terminate in an inflorescence. The latter are renewed by lateral shoots which arise immediately below the terminal inflorescence or not at all (C).

Figure 120 - **Pseudobaeckea cordata**. *Flowering shoot systems, A, two seasons old (compare with fig. 121 122),and B, three seasons old, showing sympodial and monopodial shoot connections (compare with fig. 123)*

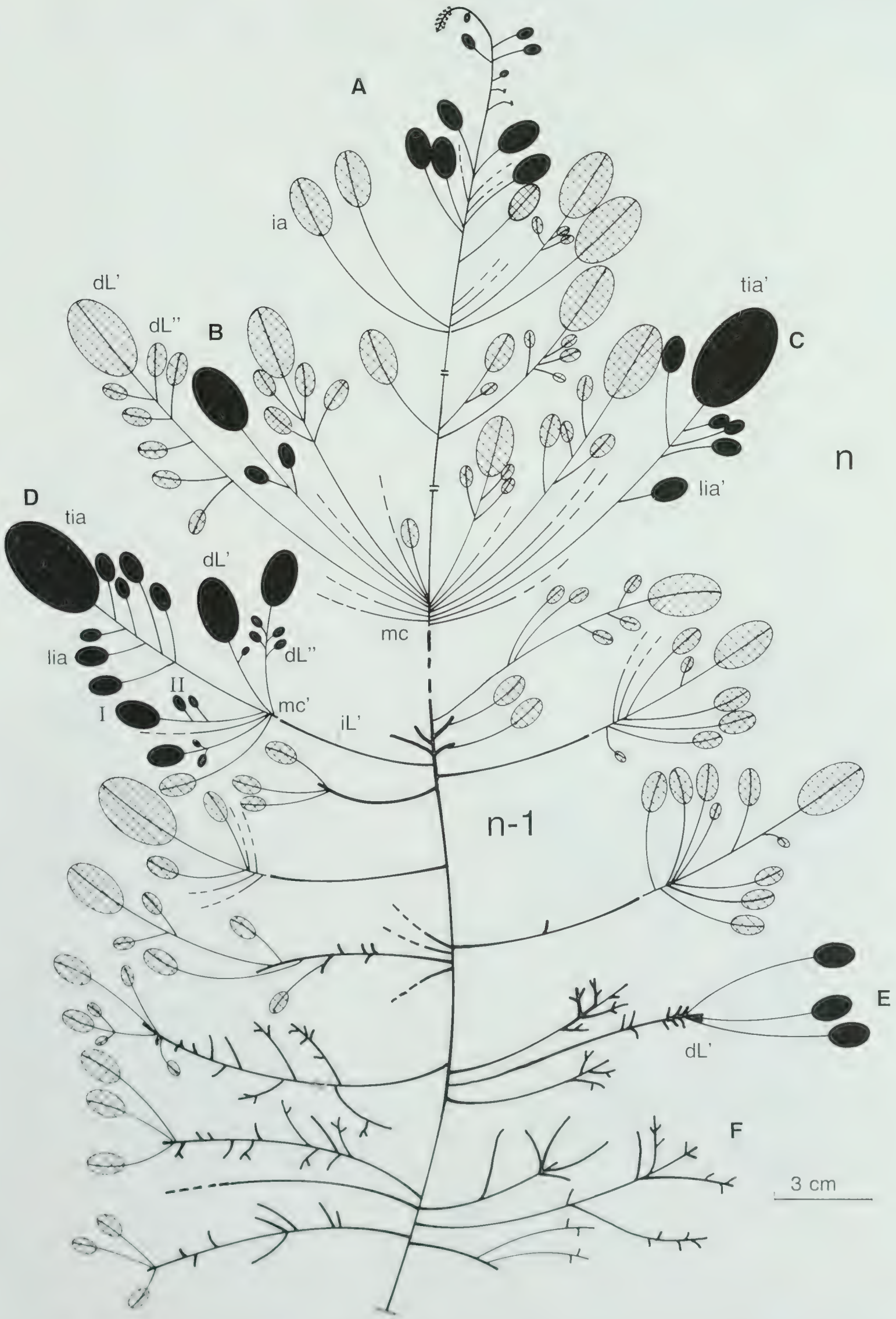


Figure 121 - **Pseudobaeckea cordata.** *Rough profile of a flowering shoot systems, two seasons old (compare with fig. 120A). The black coloured branch systems A-E are illustrated in more detail in fig. 122*
ia, *aggregate of inflorescences; the main axis of season n has been artificially reduced in length*

Lateral flowering shoots behave similarly (fig. 121,122). They usually terminate in an inflorescence which either dies off after flowering (F), or produces renewal shoots below the inflorescence (E). Very rarely, one of the lateral shoots may remain indeterminate and continue to grow on in the next season (mc').

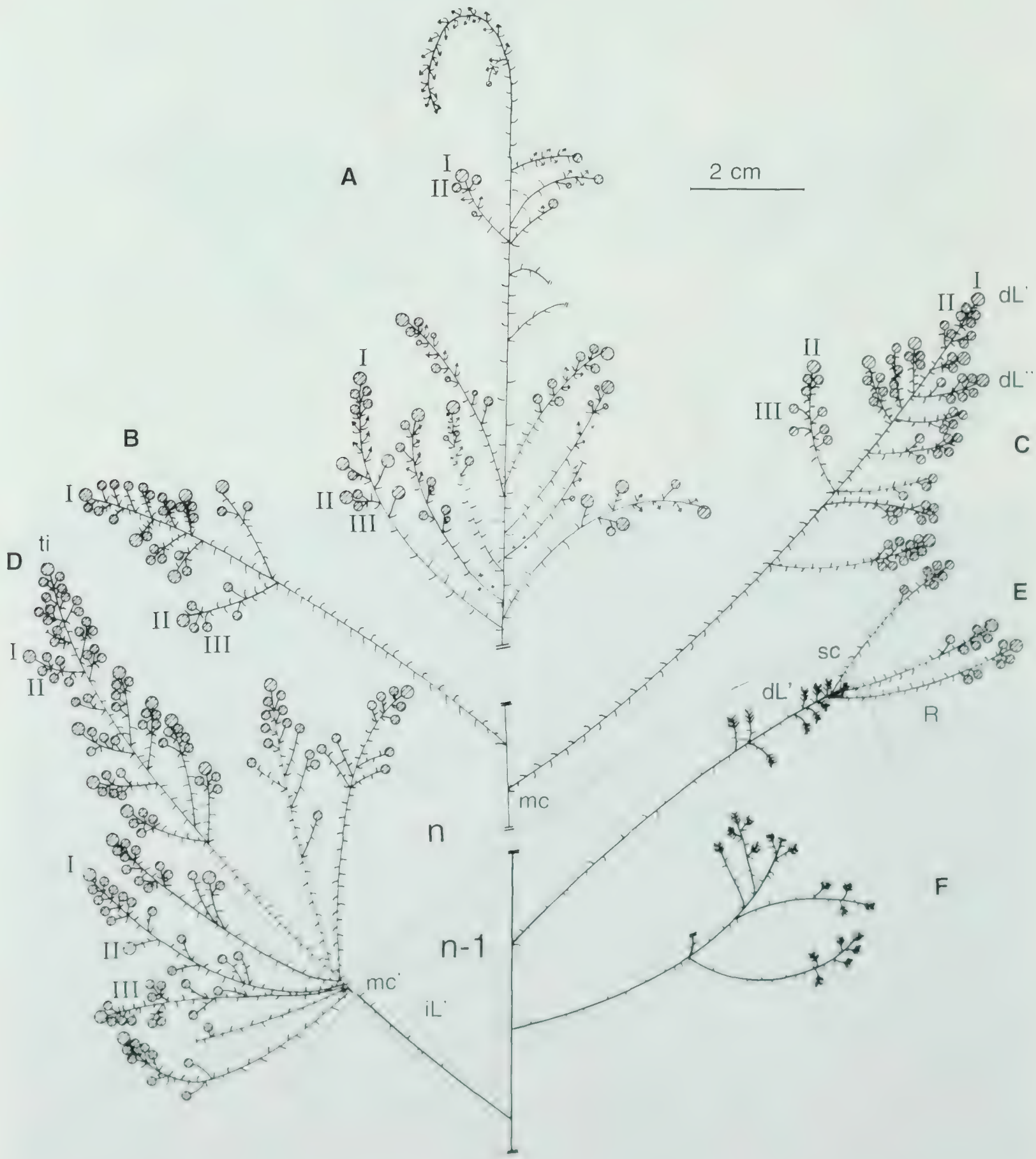


Figure 122 - **Pseudobaeckea cordata**. *Profile of some selected details from the shoot system illustrated in fig. 120A and 121. Note the monopodial connection of the two SGUs involved and the sympodial branching pattern of the lateral shoots.*

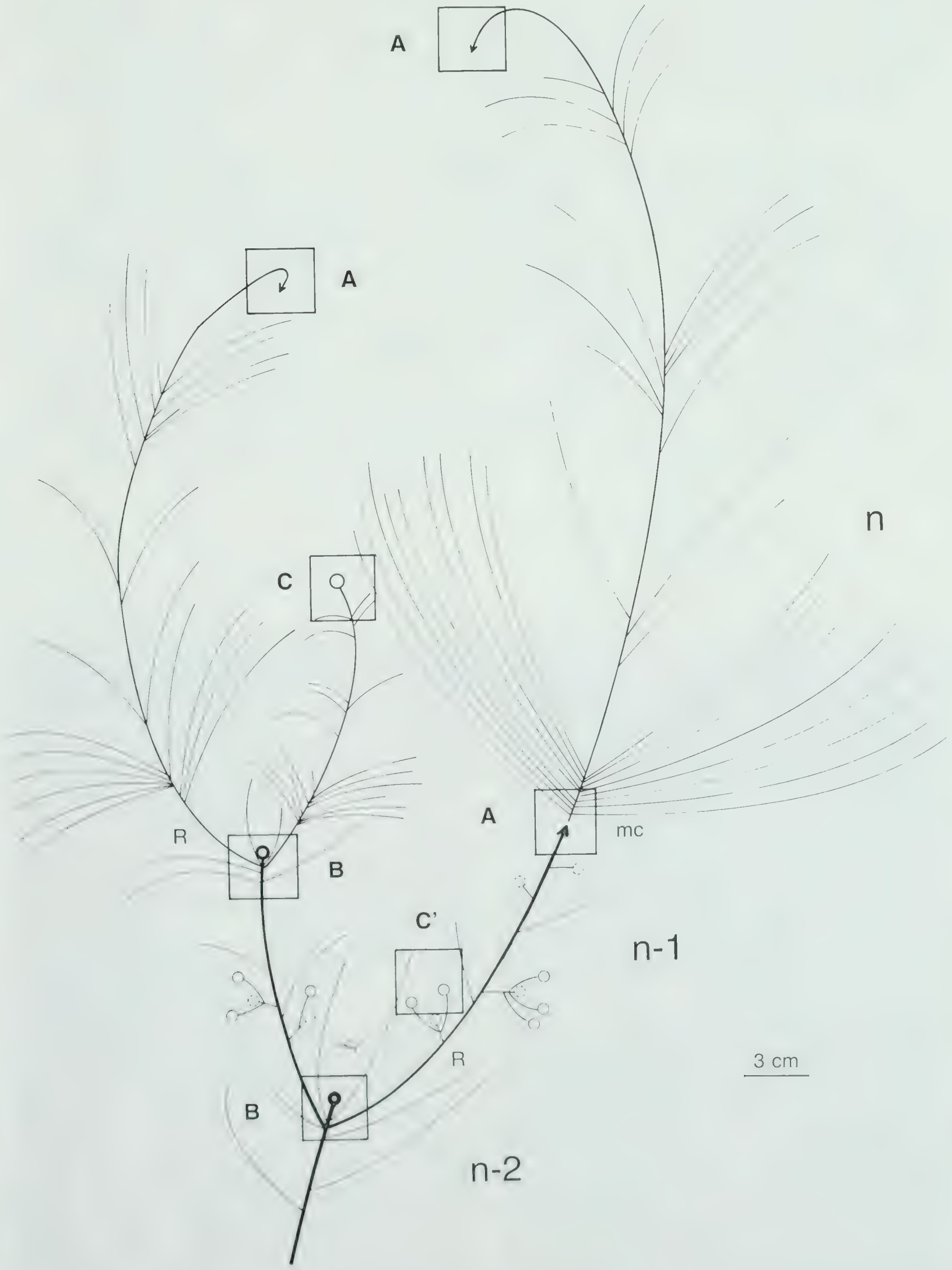


Figure 123 - **Pseudobaeckea cordata.** *Rough profile of the flowering shoot system shown in fig. 120B. A, monopodial connection of the dominant shoot, B, sympodial connection by subfloral renewal shoots, C, no renewal shoots present.*

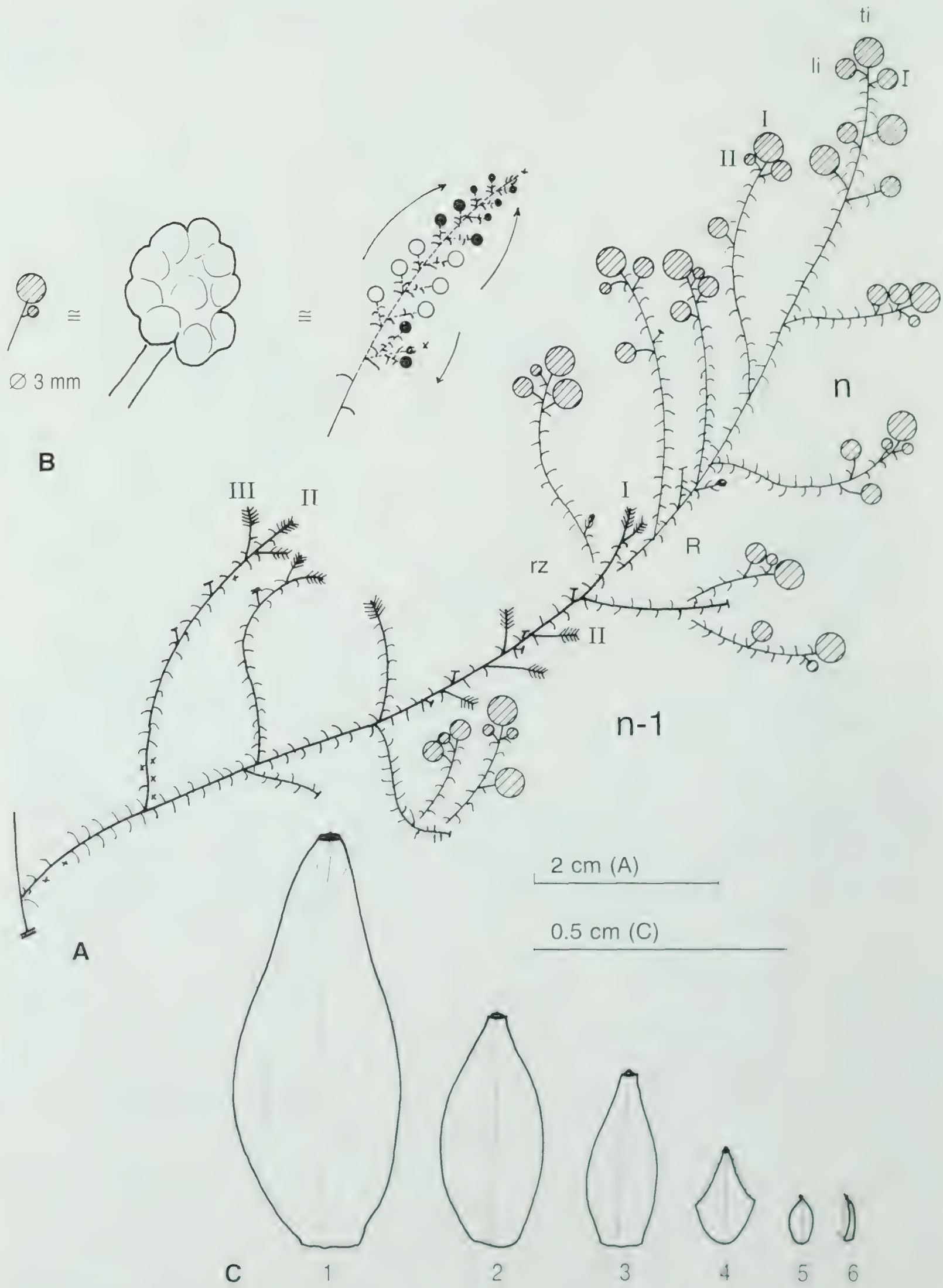


Figure 124 - **Pseudobaeckea cordata.** *A, Profile of a lateral shoot, two seasons old; note the characteristic pattern of the persistent peduncles, B, symbol, form and profile of an inflorescence showing the acropetal flowering sequence of the indeterminate terminal inflorescence and the retarded flowering of the lateral inflorescence below, C, leaf metamorphosis: 1-3, leaves from proximal to distal, 4, flower-subtending leaf, 5-6, prophylls* *Arrows in B: flowering sequence*

The lateral shoots have a lifespan of only two seasons, which may have to do with competition from successor SGUs for light and space. The result is a clear subdivision of the shrub into a flowering periphery and a woody interior. The much branched periphery only ages one season and is displaced further outwards from season to season. Only the leading shoots are incorporated into the woody interior of the shrub while the other branches are shed. In this manner the shrub grows allotropically and acquires its broad oval form.

P. africana (fig. 125B) differs from *P. cordata* in various ways: the individual SGUs are much shorter, less branched and always determinate (fig. 126B, 127A). Accordingly, both monopodial shoot connections and indeterminate lateral shoots are lacking. All shoots end in a terminal spike-like inflorescence and renew by means of five to six lateral shoots which arise from below the terminal inflorescence or among the uppermost lateral inflorescences (fig. 126C, 127A: rz). Sylleptic flowering lateral shoots appear only in the medial-distal part of the SGU, while the basal zone remains unbranched. The flowering shoots are either unbranched (I) or branched and have additional inflorescences of 2nd order of branching (II) (fig. 127B). As in *P. cordata* the lowermost shoots are the most developed so that the flowering zone acquires a pyramidal shape (fig. 127B). The shoot systems of *P. africana* are however smaller, thinner and less robust than those of *P. cordata*. They have a fan-shaped habit (fig. 126A,B) arising from incorporation of only the renewal shoots into the woody interior of the shrub and shedding of all the lateral shoots.

Figure 125 - **Pseudobaeckea.** *Flowering shoot systems: A,* P. cordata *with head-like and, B,* P. africana *with spike-like inflorescences*

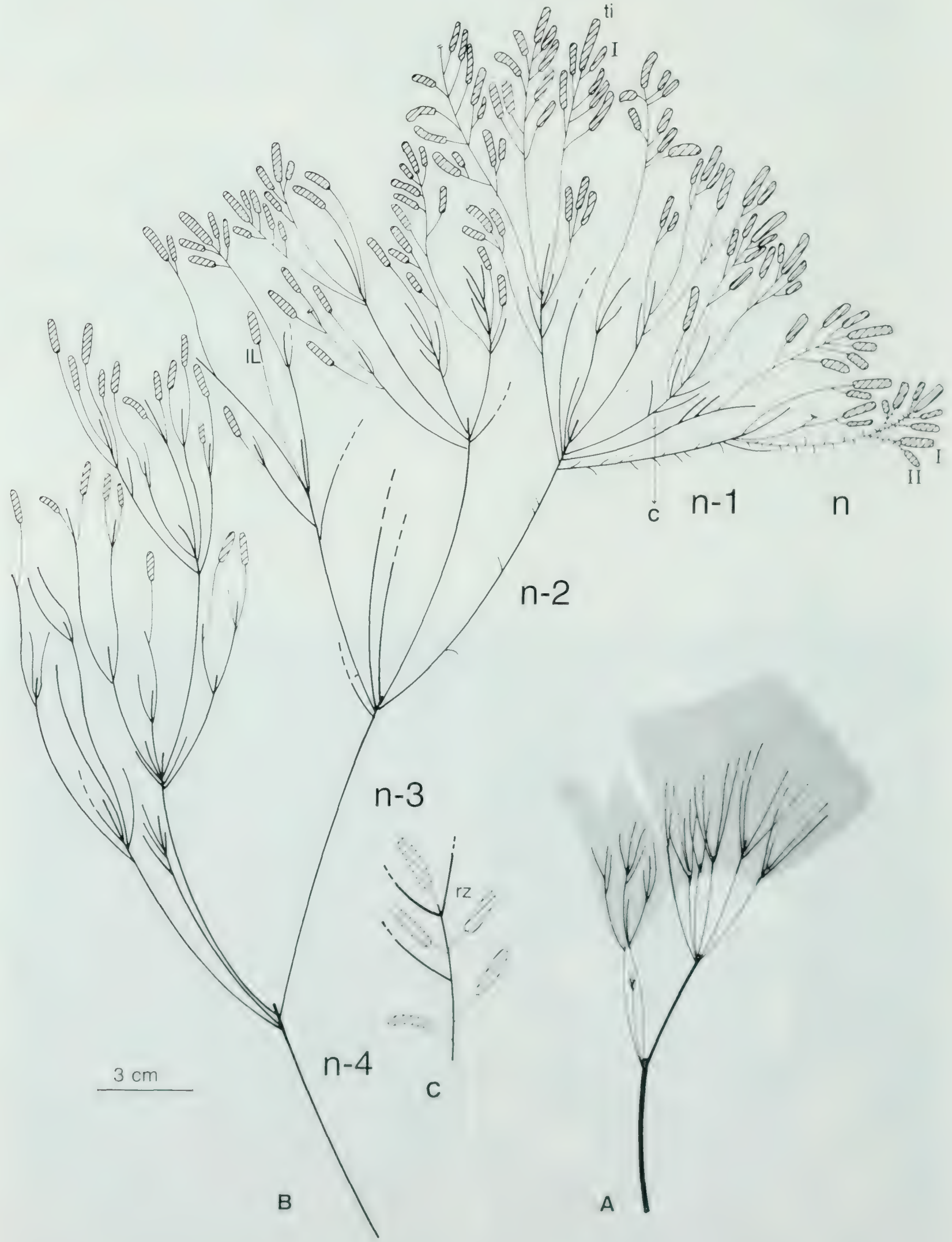


Figure 126 - **Pseudobaeckea africana**. *A, habit and, B, profile of a flowering shoot system, five seasons old, C, detail from B, reconstructed as it would have been at season n-1, showing the position of the renewal shoots below the terminal inflorescence.* IL, *late lateral shoot.*

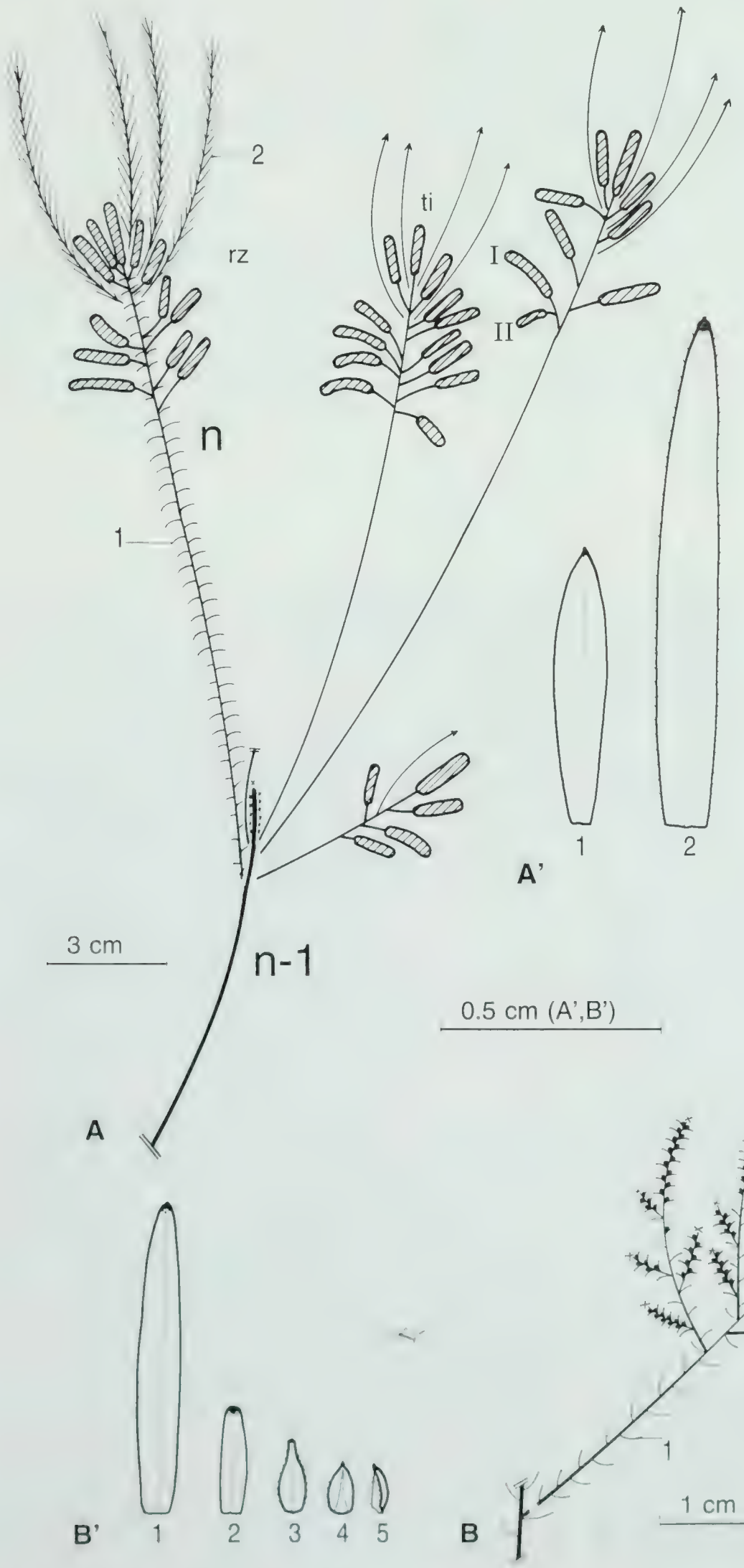


Figure 127 - **Pseudobaeckea africana**. *A, profile of a shoot system in the postfloral stage, with deflorated inflorescences and actively growing renewal shoots, A', leaf of the dominant shoot (1) and of the renewal shoot (2); B, profile of a flowering lateral shoot showing the exact number of flowers per inflorescence and the position of vegetative primordia, B', leaf metamorphosis: 1-2, leaves, proximal and distal, 3, flower-subtending leaf, 4-5, prophylls; C, profile of the inflorescence showing the acropetal flowering sequence (arrow). The numbers in A/A' and in B/B' correspond to each other.*

P. teres (fig. 128) differs fundamentally from the two species shown above. *P. cordata* and *P. africana* grow as large, erect shrubs while *P. teres* is a low, prostrate rock crevice species (fig. 3B). Today the species is known only from a single locality at the summit of Elandsberg where two plants were found in December 1996. They appeared vigorous and were in full flower. The shoot system in this species is differentiated into long leader-shoots growing plagiotropically and short flowering shoots growing orthotropically (fig. 128C,D, 129A,B). The result is a mat-like growth form with a flowering plane above and a woody interior below (fig. 128A,B).

The apex always remains indeterminate, either growing on in the next season or dying off. In the latter case subterminal lateral shoots renew the shoot system. The flowers are arranged solitarily at the end of lateral short-shoots (fig. 130A, 131A). They fall off easily leaving a circular scar. In fig. 129B a shoot system from a herbarium specimen (fig. 129A) is depicted in detail. It was not possible to identify individual SGUs because the whole shoot system was covered with minute, densely appressed and obviously persistent leaves. It proved difficult, even using fresh material (fig. 131A), to determine the age of the growth axis.

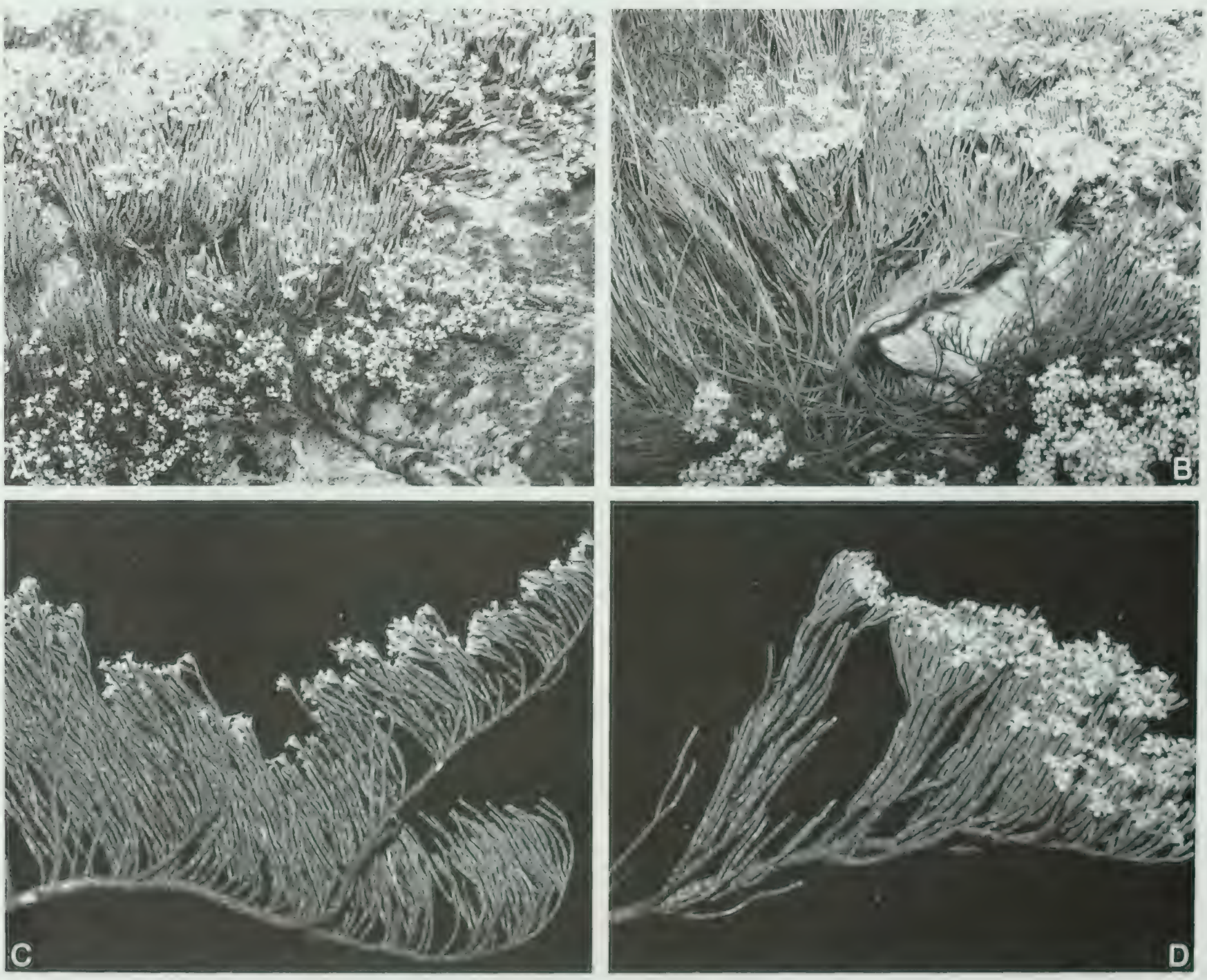
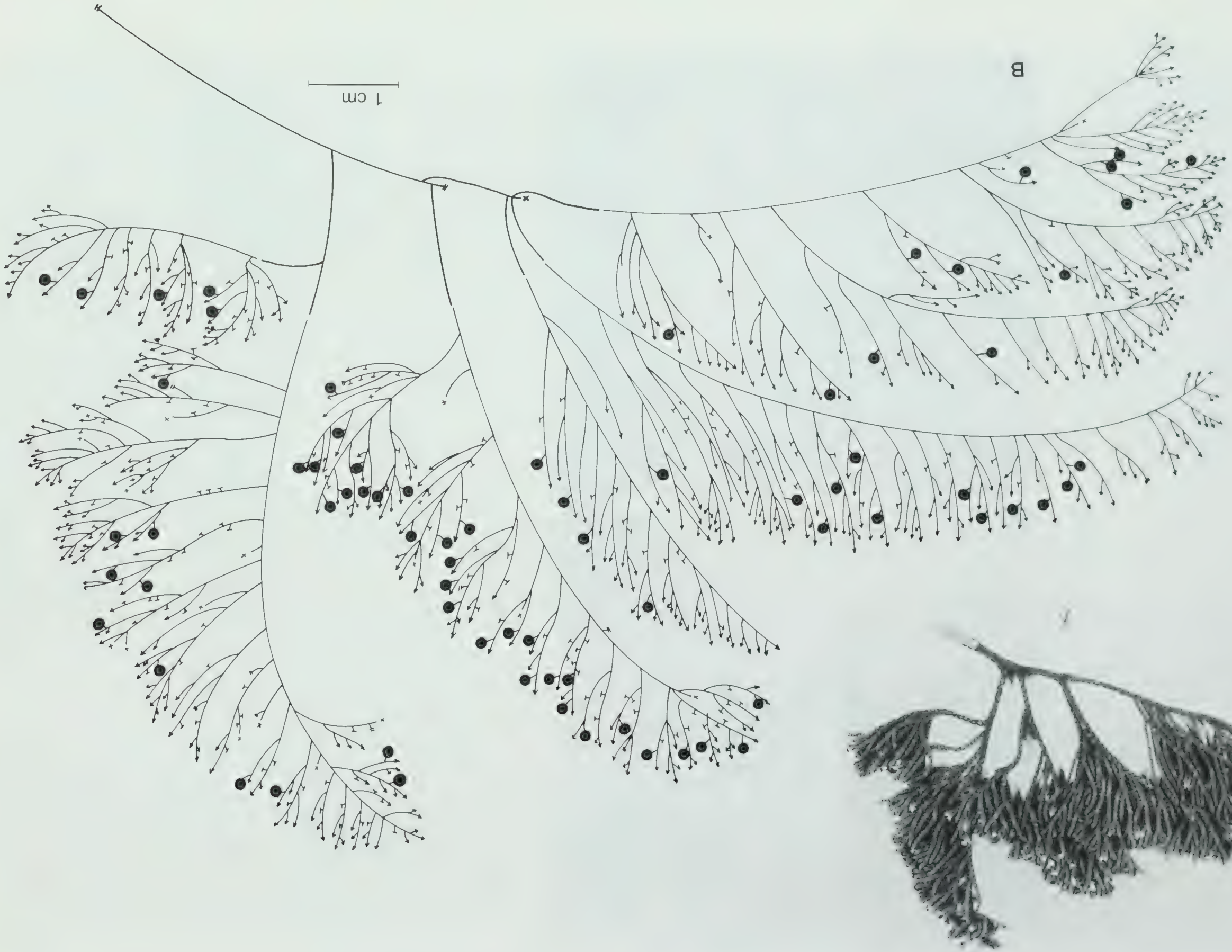


Figure 128 - **Pseudobaeckea teres.** *A,B, flowering shrub, creeping between rocks at the summit of Elandsberg, Ladismith, C,D, flowering shoot systems showing the low, prostrate growth form of the species*

Figure 129 (p. 159) - **Pseudobaeckea teres**. *A, habit (Esterhuysen 33463, B) and B, profile of a flowering shoot system, several seasons old, showing the constant lateral position of the flowering short-shoots*


B
1 cm
A

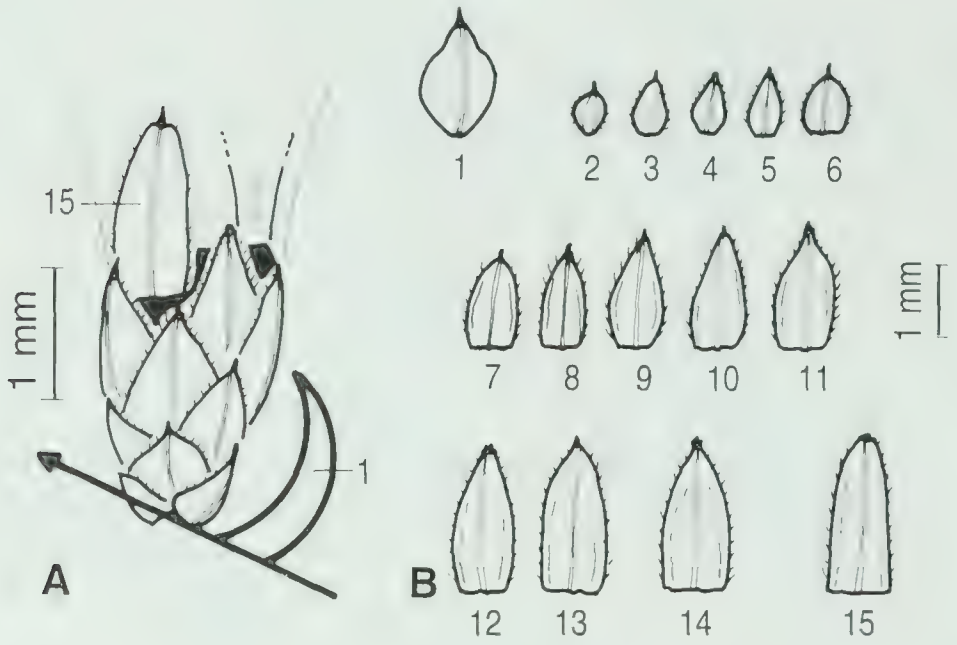


Figure 130 - **Pseudobaeckea teres**. *A, habit of a flowering short shoot showing the numerous scale-like bracts surrounding the terminal flower, B, leaf metamorphosis: 1, leaf, 2-14, bracts, 15, sepal.*

Figure 131 - **Pseudobaeckea teres.** *A, flowering shoot system showing the lateral position of the flowering bracteate short-shoots, B, flowers from above.*

Leaf metamorphosis and inflorescence structure. The inflorescences of *P. cordata* are minute (about 3 mm in diameter) and of a globular or rarely oval form (fig. 124B). The organization is indeterminate. Because of the presence of prophylls the inflorescences are regarded as truncate cephaloids. They are aggregated in clusters of various size. The terminal inflorescence (15-20 flowers) is always the largest while the uppermost lateral inflorescence (3-5 flowers) is the smallest. As regards each individual inflorescence, the flowering sequence is acropetal. However, it sometimes appears divergent (fig. 124B arrows). In this case two or more inflorescences are densely aggregated and the terminal one flowers before the lateral ones.

The leaves decrease in size from proximal to distal zone of the SGU (fig. 124C: 1-3), merging into the green flower-subtending bracts and two (rarely three) prophylls of each flower (fig. 124C: 4-6). Thus, leaf metamorphosis is gradual. The prophylls are bracteate with a green midrib and broad membranous margins.

In contrast to *P. cordata*, leaf metamorphosis is abrupt in *P. africana* (fig. 127B´). The unbranched proximal part of the SGU bears leaves which are twice as big as those found at the branched distal part (1,2) while the differences between the distal leaves and the flower-subtending leaves and prophylls are minimal (2-5). As fig. 127A´ illustrates, the leaves of the renewal shoots may be much larger than those of the preceding SGU. This is an example of the well known variability of the leaf size in *P. africana* and *P. cordata* (Pillans 1947:139,142; Carlquist 1991:7,28).

The inflorescences of *P. africana* (fig. 127C) show the same organization as in *P. cordata*. However, they have up to 50 flowers and are accordingly more elongated.

P. teres has solitary flowers borne at the end of lateral bracteate short-shoots (fig. 130A, 131A). Compared with the respective leading shoots, they are for the most part correlated with branches of 2nd order or more rarely with those of 1st or 3rd order of branching. Occasionally two flowers are borne on the same shoot, but are always clearly separated by several leaves. The flowering short-shoots are subtended by a normal leaf (fig. 130B: 1) and bear 12-13 scale-like bracts (fig. 130B: 2-14) which latter densely surround the terminal flower. The bracts gradually increase in size, become thinner in texture and merge into the sepals (fig. 130B: 15) which are also spirally arranged. In general, the flowering short-shoots of *P.teres* may be said to resemble those of *Audounia capitata* in being laterally arranged and covered with scale-like bracts (fig. 6B, 11, 12).

Summary. As fig. 132 illustrates, two models are necessary in order to describe the branching and flowering patterns of the genus *Pseudobaeckea*, one for *P. cordata* and *P. africana* (A-C) and a second for *P. teres* (D).

The reference system (RS) of *P. cordata* and *P. africana* (A) is subdivided into a terminal inflorescence (ti), a subfloral renewal zone (rz) and an extended branching zone (bz), with sylleptic flowering lateral shoots (sfL) of 1st to 3rd order branches (I-III) and sylleptic vegetative lateral shoots (svL). The individual inflorescences are truncate head- and spike-like cephaloids with acropetal flowering sequence. They comprise about 15-40 flowers in *P. africana* and only 3-20 flowers in *P. cordata*. Each flower is subtended by a leaf and two (to three) prophylls. The connection of the SGUs is strictly sympodial in *P. africana* (five or six renewal shoots) and mostly sympodial in *P. cordata* (two renewal shoots). The renewal shoots arise mainly from below the terminal inflorescence, but occasionally are interspersed with the uppermost flowering shoots of the branching zone.

In *P. cordata* the terminal inflorescence is occasionally lacking and the apex of the dominant shoot is seen to grow on in the next season (B: mc). Well developed lateral shoots may mimic the parent axis in this respect (C: iL´,mc´). The branching zone as seen in *P. africana* is less well-developed than in the RS and may be entirtely lacking (C: *R*). Late flowering shoots rarely appear in this species (C: lL).

The model of *P. teres* (D) is difficult to reconstruct. However, the regular pattern shown in fig. 132D: β appears to be repeated within the shoot systems analyzed which can be interpreted as being several season old and connected in a monopodial manner. Where the apex dies off, renewal shoots are formed which clearly arise above the lateral flowering short-shoots. A model can be presented (D: α) which shows the existence of a vegetative apical zone (az), a subterminal renewal zone (rz) and a branching zone (bz) with lateral flowering short-shoots.

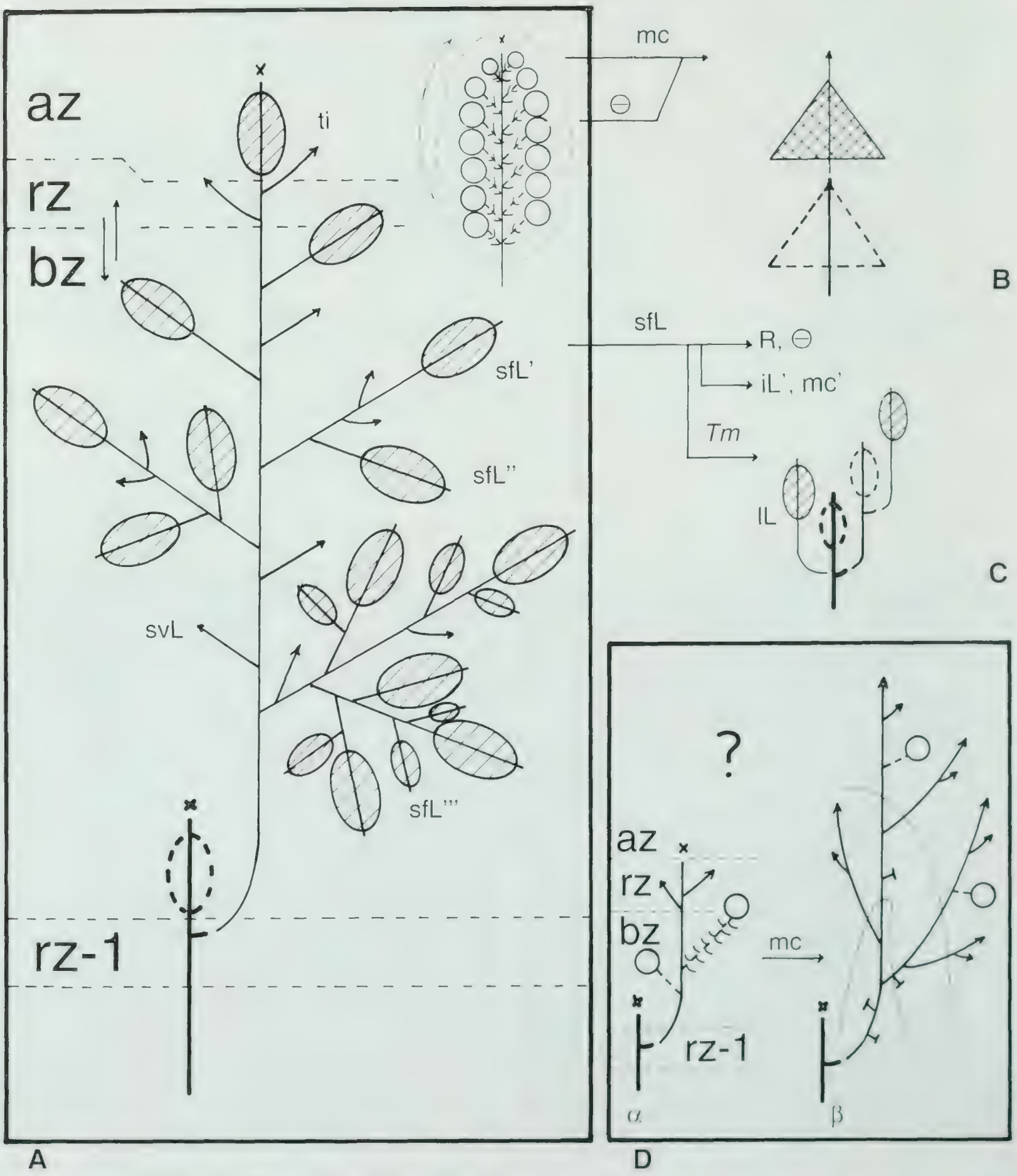


Figure 132 - ***Models for the genus*** **Pseudobaeckea,** *A-C, for* P. cordata *and* P. africana, *D, for* P. teres. *A, reference system (RS) showing the apical zone bearing a terminal truncate cephaloid, the renewal zone below and a zone of multiple branching with vegetative and flowering lateral shoots. B,C, variation of the RS showing the absence of the terminal inflorescence and the growing activity of the apex (B) and the reduction of the branching zone, the presence of indeterminate and of late lateral shoots (C). D, branching and flowering behaviour in* P. teres *(β) and reconstruction of the corresponding RS (α).* lL, *late lateral shoot*

3.9 *Raspalia* Brongn.

Raspalia *is the largest genus of the Bruniaceae (sixteen species), including rock-crevice species, shrubs of medium size and erect shrubs up to three meters in height.* Raspalia *is confined to fynbos vegetation in the Western Cape with one outlier (*R. trigyna) *in Natal-Kwazulu (fig. 1A:arrow).*

R. globosa, R. microphylla *and* R. virgata *were studied in their natural habitat. Fresh material of* R. sacculata *was provided by Elsie Esterhuysen. Herbarium material of a further eight species was included in the present study.*

Growth and branching pattern. According to the branching pattern and arrangement of the inflorescences, the twelve species studied form two groups. The first group is characterized by terminal inflorescences and a clear sympodial branching pattern while the second group often lacks the terminal inflorescence and continues growth in a monopodial manner. The result of the different modes of branching is either a polyaxial or a monoaxial habit.

The first group is represented by *R. globosa, R. stokoei, R. staavioides, R. sacculata, R. villosa* and *R. virgata.*

- Shrubs of *R. globosa* reach a height of about one meter (fig. 133A,B). The inflorescences are globular and the young shoots characteristically white tomentose (fig. 134). The flowering periphery of the shrub (fig. 135) is composed of short (two to five centimetres long) SGUs which arise below the terminal inflorescence of the mother axis concerned (rz-1). They are unbranched in the proximal part, bear one or two, (occasionally up to eight) flowering short-shoots in the medial part (sfL) and a renewal zone (rz) below the terminal inflorescence (ti). The shoot system is renewed by two to four renewal shoots which begin growth syllepticaly (fig. 134B: sR), but continue to grow and to flower in the next season. The result is a regular forked branching pattern with individual leading shoots. The leading shoots are characterized by both their increased length and number of lateral flowering short-shoots. Rarely, a lateral short-shoot may exhibit a renewal zone of 1st order of branches below its terminal inflorescence (rz′) but branches of 2nd order have never been found.

Figure 133 - **Raspalia globosa** *at Nuweberg Forest Reserve.*

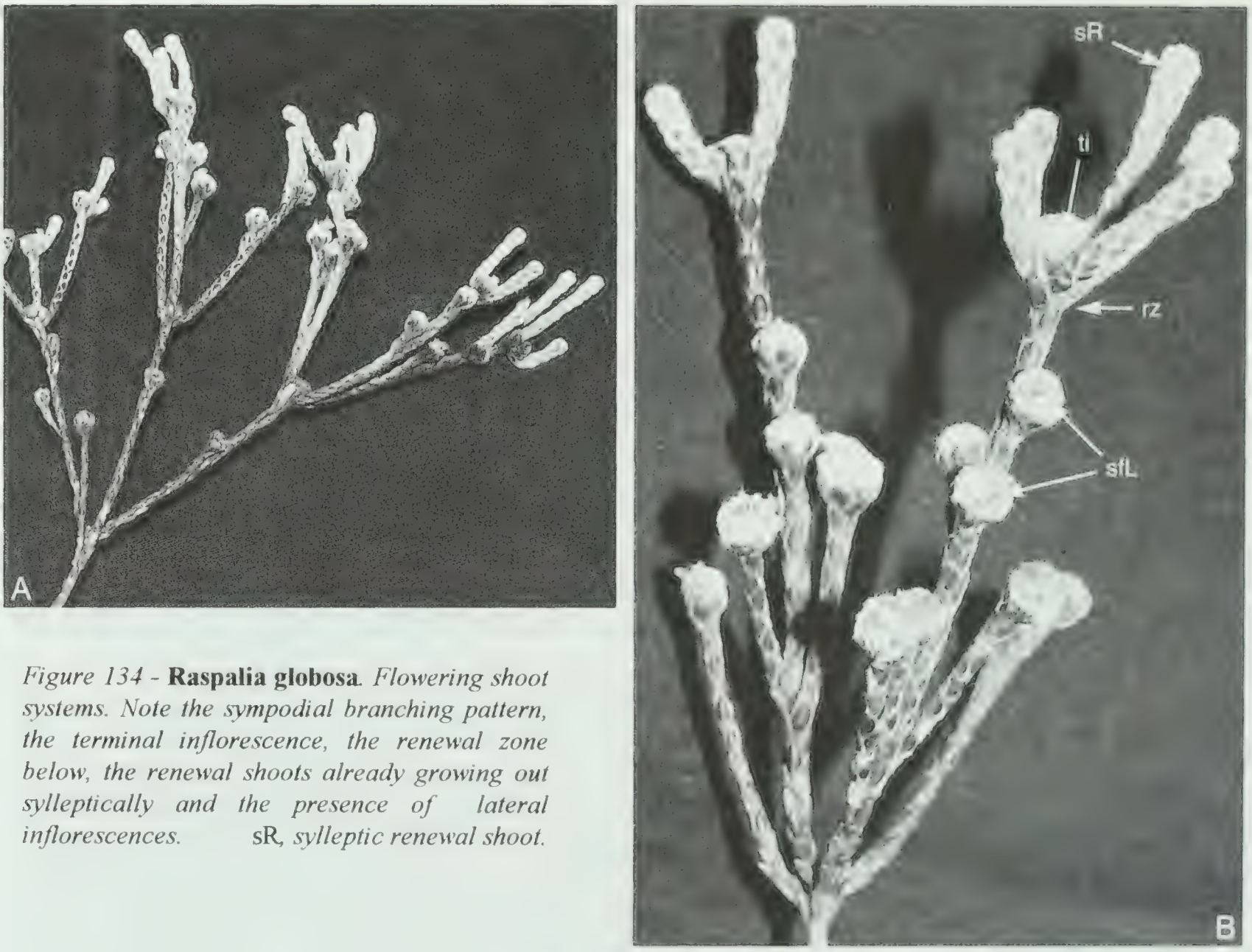


Figure 134 - **Raspalia globosa**. *Flowering shoot systems. Note the sympodial branching pattern, the terminal inflorescence, the renewal zone below, the renewal shoots already growing out sylleptically and the presence of lateral inflorescences.* sR, *sylleptic renewal shoot.*

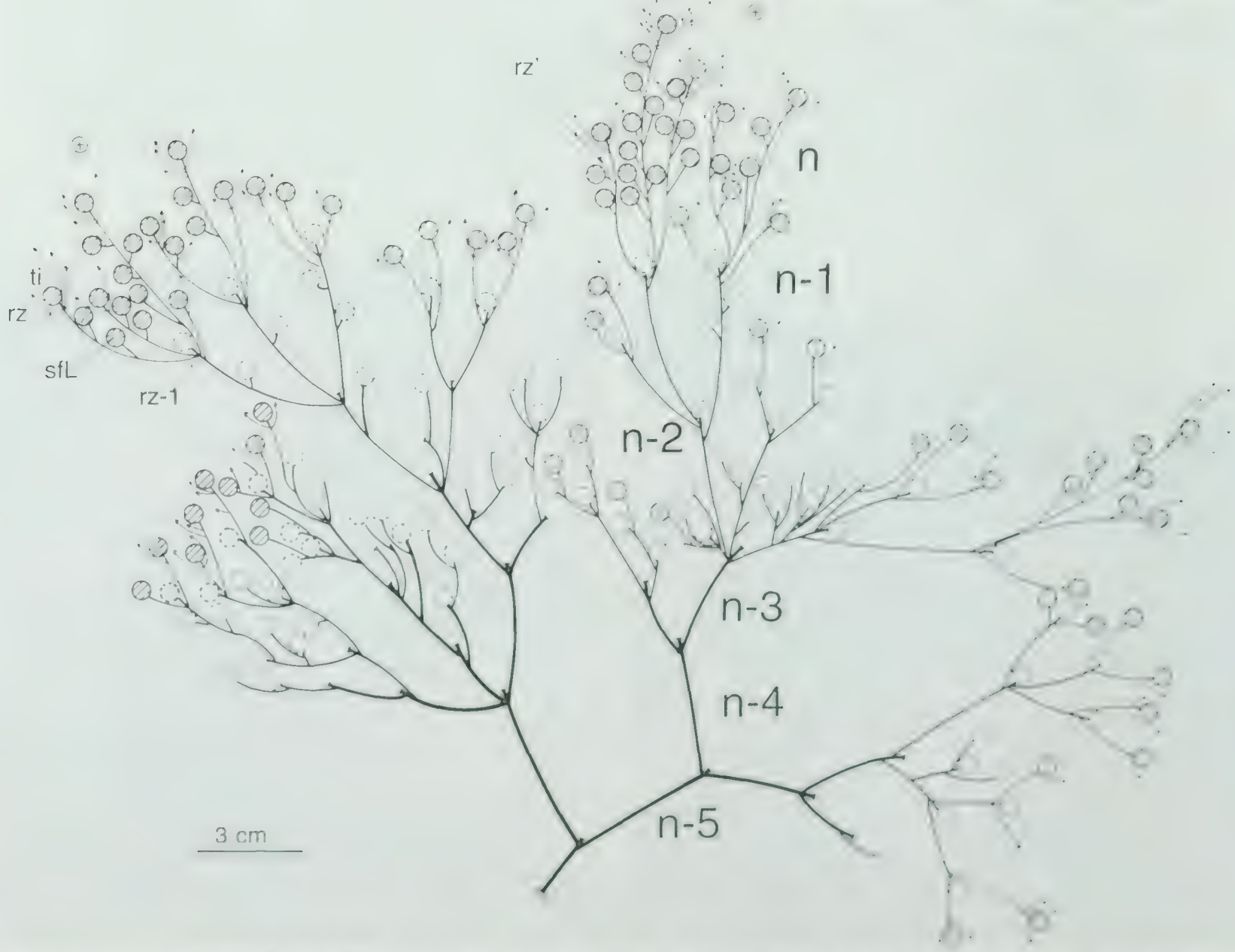


Figure 135 - **Raspalia globosa**. *Profile of a flowering shoot system, six seasons old. Note the regular sympodial branching pattern with one sympodial unit per season*

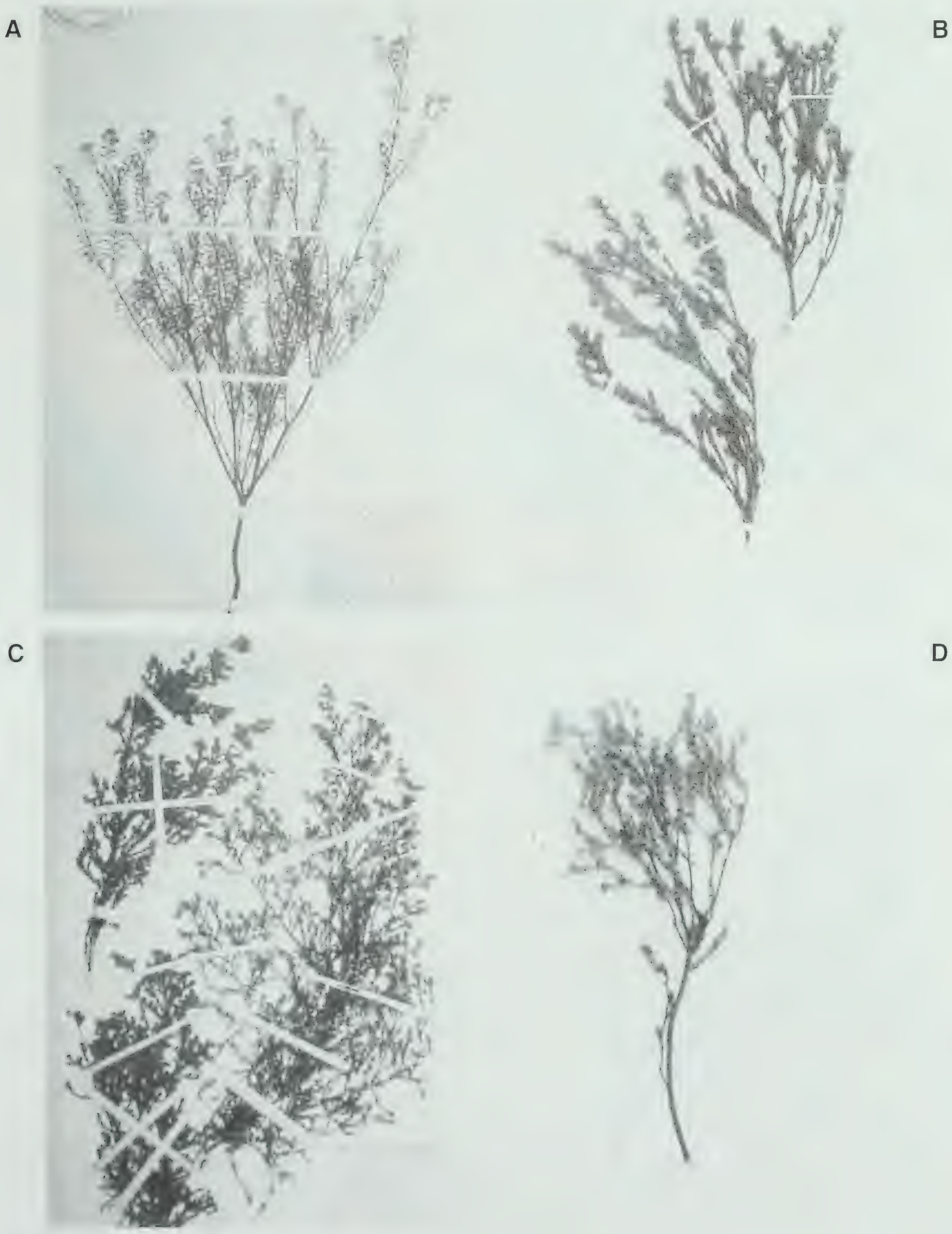


Figure 136 - **Raspalia**. *A*, R. staavioides *(Powrie 136, NBG)*, *B*, R. sacculata *(Esterhuysen 26512, B)*, *C*, R. villosa *(Esterhuysen 7376, NBG)*, *D*, R. stokoei *(Carlquist 5053, B)*.

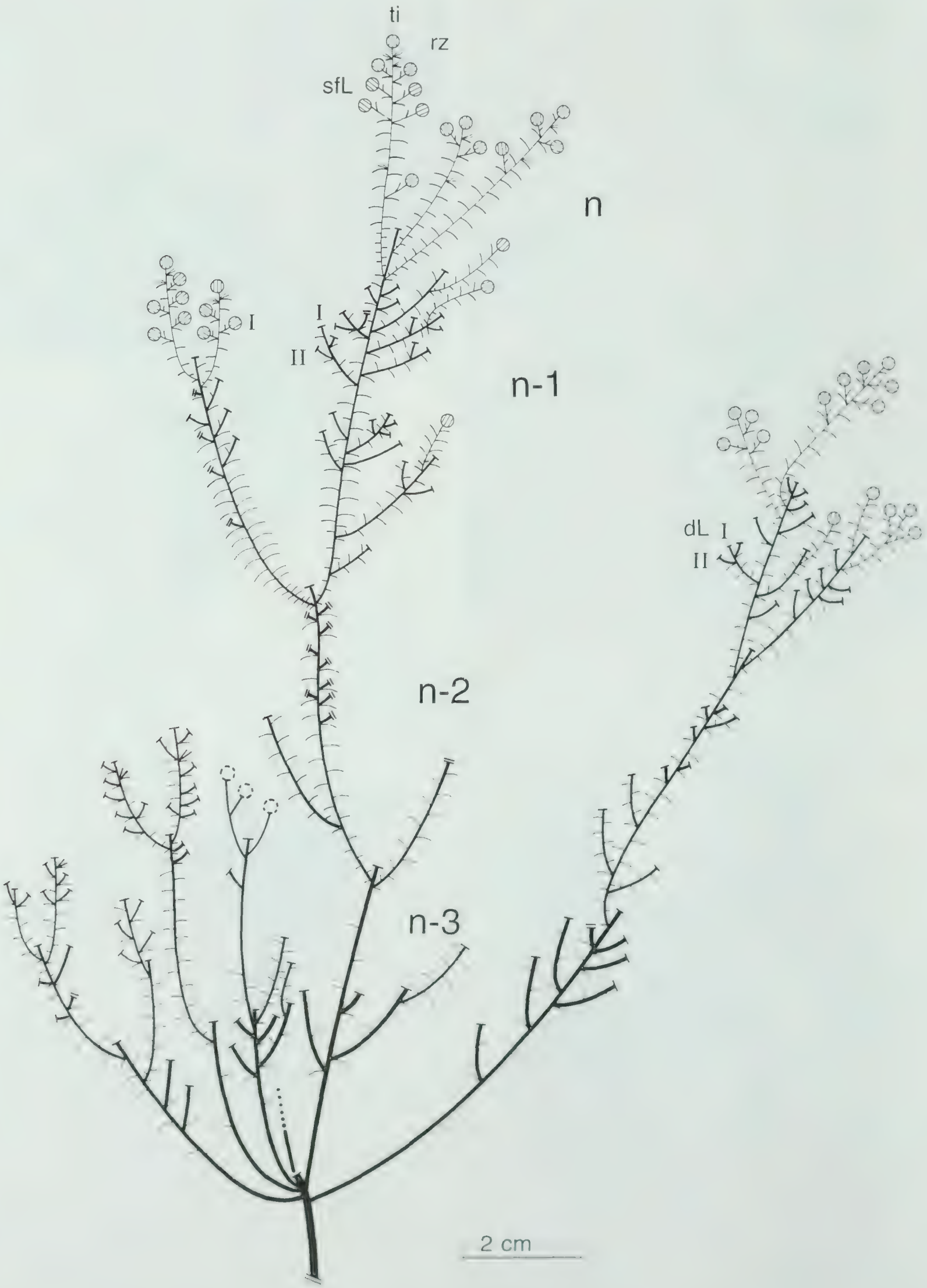


Figure 137 - **Raspalia staavioides**. *Profile of a flowering shoot system, four seasons old. Note the regular sympodial branching*

- *R. staavioides* (fig. 136A, 137), *R. sacculata* (fig. 136B, 138) and *R. villosa* (fig. 136C, 139) have a similar growth and branching pattern to *R. globosa*. However, they show more sylleptic flowering lateral shoots per SGU, which may be branched and then bear inflorescences of 2nd order of branches (fig. 137-139: sfL, dL′, I,II).
- In contrast to the species above, which usually reach a height of 60-90 cm (in *R. staavioides* up to 150 cm), the shrubs of *R. stokoei* (fig. 136D, 140) are very low (up to 30 cm in height), while *R. virgata* (fig. 141, 144A) may attain a height of up to 3 m (Bond & Goldblatt 1984: 209/210). *R. stokoei* bears short SGUs, one to three centimetres in length, which always end in a terminal inflorescence and only rarely show additional lateral flowering short-shoots (fig. 140).

R. virgata, in the typical case, is characterized by slender shoots, but dependent on age and/or habitat conditions a more dense branching pattern be present (fig. 144A). One or two of the (up to six) cataleptic lateral shoots arising from the renewal zone below the terminal inflorescence are much longer than the remainder and become the renewers of the shoot system (fig. 141C,D, 142: cR). Usually the proximal shoot of the renewal zone is the leader while the second renewal shoot arises among or above the remaining lateral shoots (fig. 142). The latter end in a terminal inflorescence and may bear up to seven sylleptic flowering lateral short-shoots (fig. 142: n). Occasionally the flowering short-shoots overtop the terminal inflorescence (fig. 142: o). The lateral shoot system may persist for up to three years and then die off. With increasing age branching capacity decreases and is often displaced from the main axis of the SGU to the flowering short-shoots of 1st order of branches (fig. 142: rz′). The renewal shoots are at least twice as long as the lateral shoots and unbranched in their proximal part (fig. 141C,D). Sylleptic branching starts only in the upper half, whereby the flowering zone of the renewal shoots is exposed above the level of the remaining lateral shoots. The result is an arrangement in tiers of flowering zones of the same age (fig. 141, 142: n,n′).

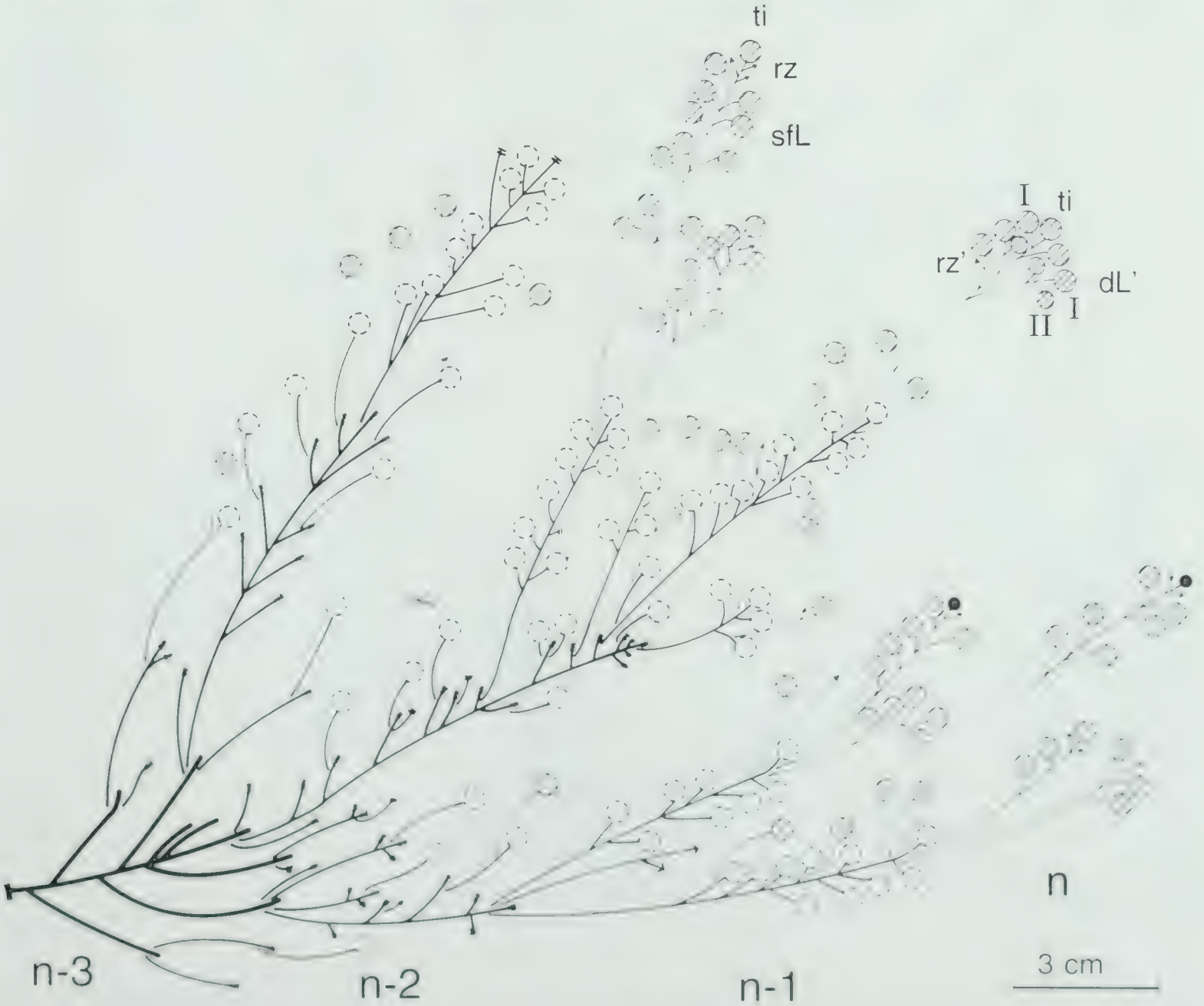


Figure 138 - **Raspalia sacculata**. *Profile of a flowering shoot system, four seasons old.*

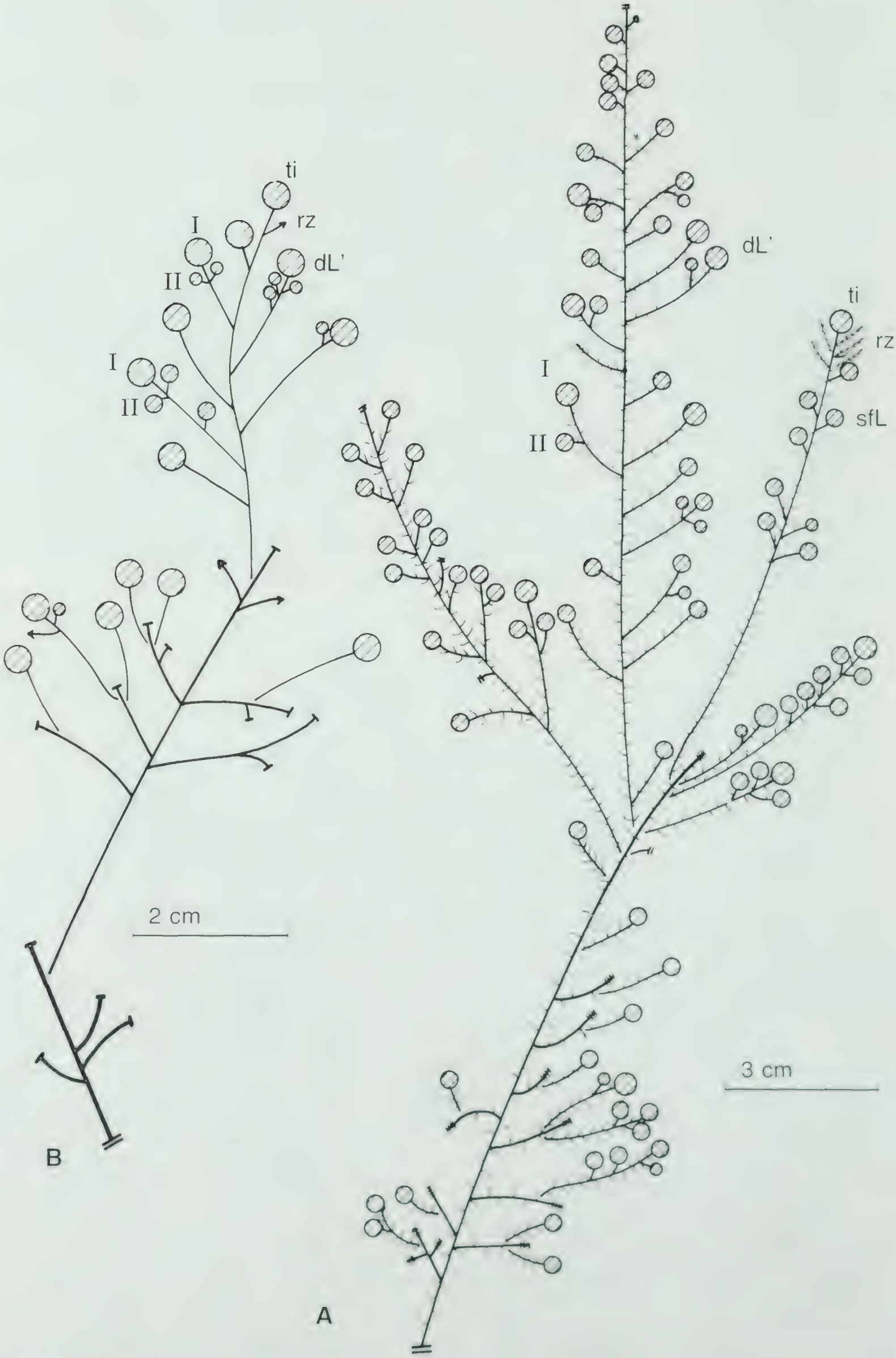


Figure 139 - **Raspalia villosa**. *Profile of flowering shoot systems.*

Besides the sylleptic lateral shoots additional cataleptic lateral shoots (fig. 142:cfL) appear in the medial part of the renewal shoots, these are comparable to the short lateral shoots of the renewal zone.

Profiles of seedlings of *R. virgata* are shown in fig. 143. The primary shoot (P) always ends in a terminal inflorescence (ti) but it is not clear at what age the apex becomes reproductive. The primary shoot is unbranched or forms lateral shoots in its medial-distal part (fig. 143B: sfL), these behave like the main shoot and thus increase the sympodial shoot system.

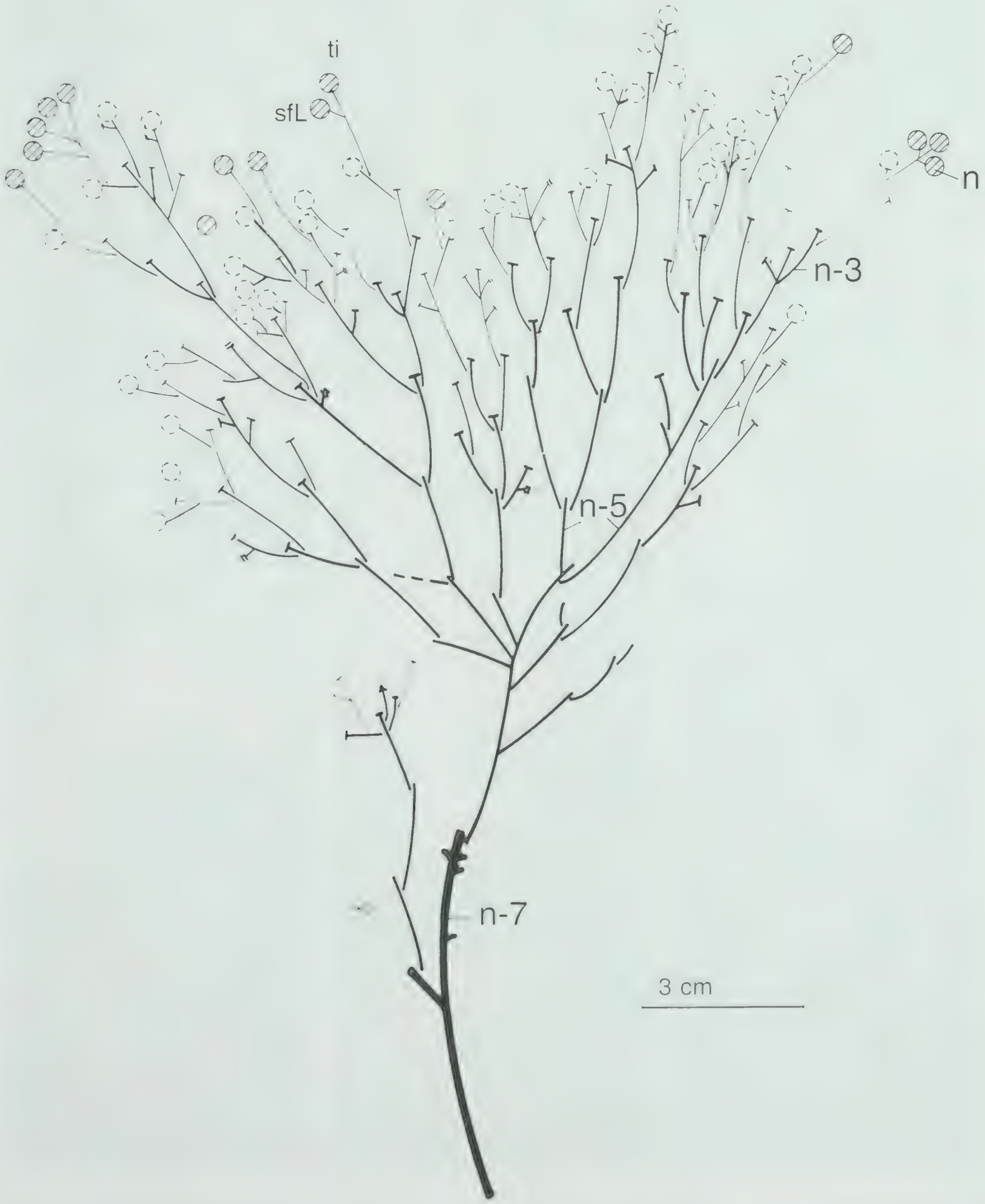


Figure 140 - **Raspalia stokoei**. *Profile of a flowering shoot system, eight seasons old. Note the short SGUs and the regular sympodial branching*

Figure 141 - **Raspalia virgata**. *A, flowering shrub at Grootberg (Grootvadershos Forest Station), B-E: flowering shoot systems showing the numerous small inflorescences and the characteristic branching pattern (C,D) caused by the presence of both short and dominant shoots.*

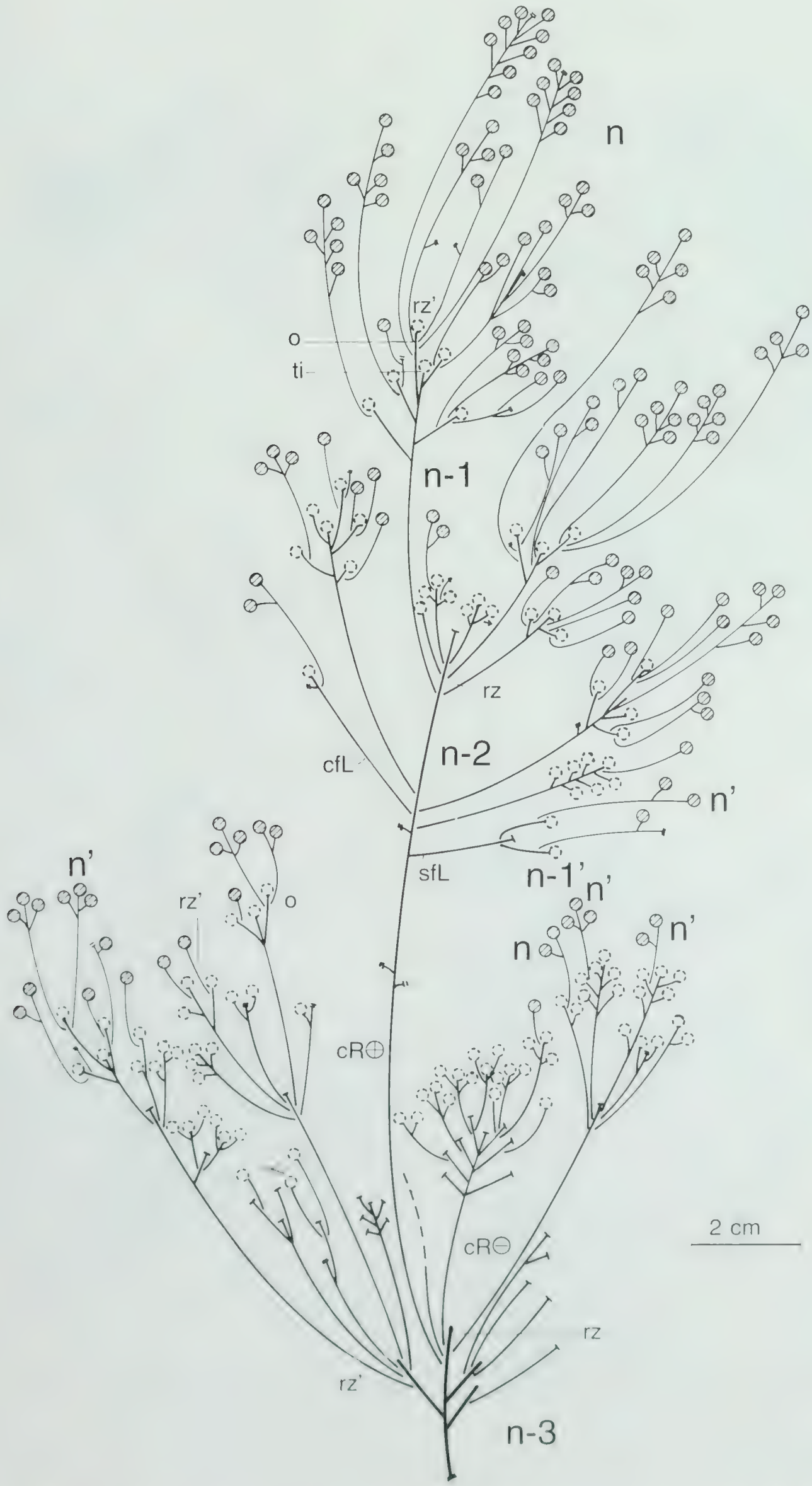


Figure 142 - **Raspalia virgata**. *Profile of a flowering shoot system, four seasons old. Note the different length of the renewal shoots resulting in a shoot-dimorphism between short and dominant shoots.* o, *overtopping.*

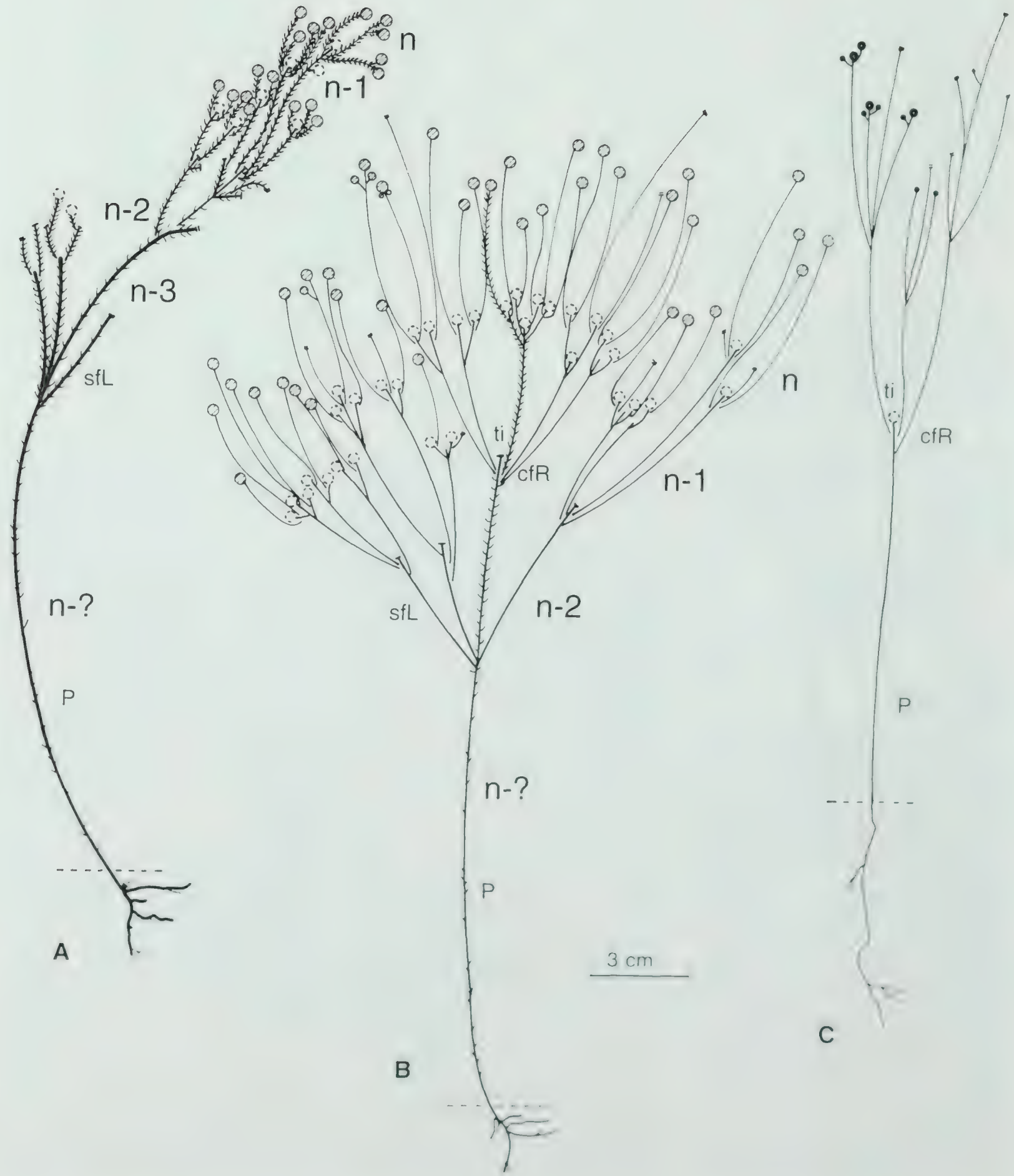


Figure 143 - **Raspalia virgata**. *Profiles of seedlings. Note the equal length of the renewal shoots in B*
P, *primary axis*

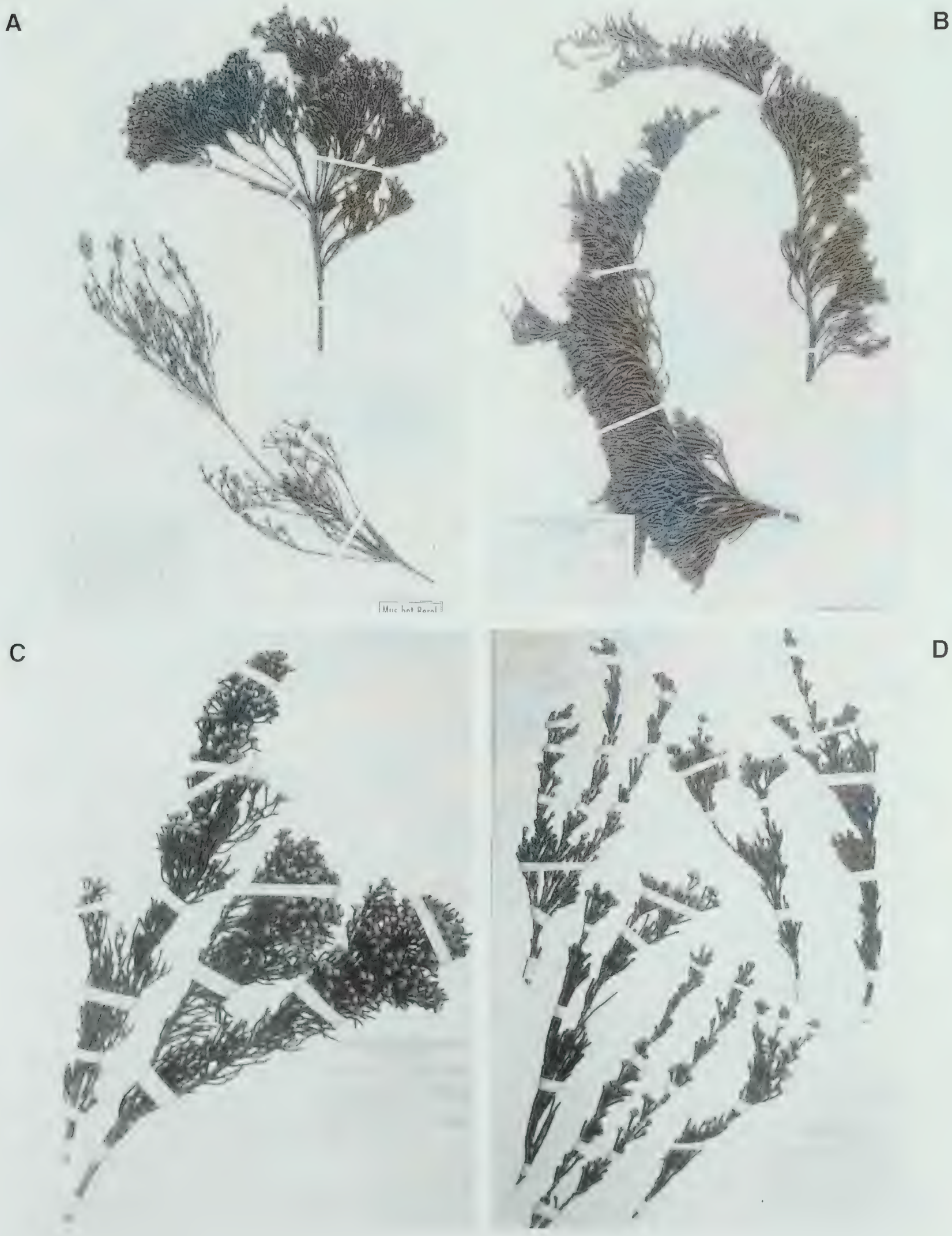


Figure 144 - **Raspalia**. *A*, R. virgata *(Powrie 33, B)*, *B*, R. variabilis *(Rourke 711, B)*, *C*, R. angulata *(Kies s.n. (6.1.1941), NBG)*, *D*, R. phylicoides (Bond s.n., NBG).

The second group is represented by *R. microphylla, R. variabilis, R. phylicoides, R. angulata, R. schlechteri* and *R. trigyna*. *R. microphylla, R. variabilis* and *R. angulata* grow in rocky habitats (Bond & Goldblatt 1984:209/210). The variable habitat conditions directly influence the growth form of the shrubs, which are usually erect with long sprouting shoots, but occasionally more compact with very short branches.

- The shrubs of *R. microphylla* studied (fig. 145A,B) were about one meter in height and characterized by long sprouts. The basal parts of the plants were leafless and composed of persistent dominant shoots, while the flowering tops were much branched and bore numerous inflorescences (fig. 147).

  A flowering shoot-system representing four seasons is shown in figures 148-150. Usually two subterminal renewal shoots are formed in case the apex of the leader shoot concerned dies off. These persist for three or four seasons before the apex dies off and the shoot system is renewed by means of lateral shoots (rz). Each SGU is densely covered with numerous short lateral shoots of about the same length (fig. 147D) which either terminate in an inflorescence or are indeterminate (fig. 149,150: dL, iL). All lateral shoots except for a few distal ones are further branched and bear sylleptic flowering, unbranched short-shoots of 2nd order of branches (II) . The lateral shoots often continue to grow on for several seasons. The indeterminate shoots grow on terminally for one or two seasons (monopodial manner) until they become determinate by a terminal inflorescence, while the determinate shoots are able to continue their growth only once they have a renewal zone of 1st order below their terminal inflorescence (sympodial way) (fig. 150: ti´, rz´). The long leading shoots often grow in a plagiotropic orientation (fig. 147A,C, 148). In this case, the lateral shoots are arranged in an orthotropic manner (fig. 150). The epitonic shoots are more branched than the hypotonic ones and tend to remain indeterminate at least in the first season.

  To sum up, the characteristic habit of *R. microphylla* is the result of a sympodially branched shoot system, the sympodial units of which are each composed of several individual SGUs connected in a monopodial manner (fig. 148. SU, SGU, mc). By this means, the long sprouts appear which clearly differ from the relatively short lateral shoot systems. The impression of an irregular arrangement of indeterminate and determinate lateral shoots probably expresses a positional influence on the branching behaviour of the plant.
- As regards branching pattern, *R. variabilis* is very similar to *R. microphylla* (fig. 144B, 151). However, it is not clear how often a leader shoot grows on in a monopodial manner. In contrast to *R. microphylla* the lateral shoots are always determinate (dL), less branched and of different length. Occasionally even the leader shoot ends in a terminal inflorescence (ti).
- *R. angulata* (fig. 144C) is also characterized by monopodially connected SGUs and sympodially branched lateral shoot systems (fig. 152A: mc, 152B´). The leader shoots are much branched and show a conjunct-acrotonic promotion of the lateral shoots. The renewal zone (rz) arises subterminally. It is not clear whether the apex dies off or produces a terminal inflorescence. As fig. 152B´ illustrates, the renewal shoots do not always become leader shoots but may also branch in a regular sympodial manner. The lateral shoots usually end in an inflorescence and remain unbranched (fig. 152A: sfL). Only some of them have a renewal zone of 1st order below the inflorescence (rz´) and are able to continue growth in a sympodial manner. Very rarely, a lateral shoot may be indeterminate (iL) and bear sylleptic flowering shoots of 2nd order.
- *R. phylicoides* (fig. 144D) is characterized by a sympodial, mainly dichasial branching pattern of the leader shoots. As in the case of *R. microphylla* and *R. virgata*, the cataleptic lateral shoots of the renewal zone are dimorphic, that is two or three of them become the renewers of the shoot system while the three to five remaining shoots are much shorter (fig. 153). The latter have a few sylleptically flowering, lateral short-shoots and always bear a terminal inflorescence. Because of the differences in the age of leaves and inflorescences it is supposed that the leader shoots are composed of several monopodially connected SGUs (mc). It is not known whether their apices develop inflorescences or die off in a vegetative condition. The long shoots are covered with numerous sylleptically flowering lateral shoots (sfL) which are always unbranched and persist for only one season. The characteristic habit of the shrubs is the product of long and slender leader shoots together with much branched renewal zones

Figure 145 - **Raspalia microphylla**. *Flowering shrubs at Nuweberg Forset Reserve (A) and at Landrostkop, Hottentot Holland Nature Reserve (B).*

Figure 146 - **Raspalia microphylla.** *Cutting under propagation at the nursery of the National Botanic Garden Kirstenbosch*

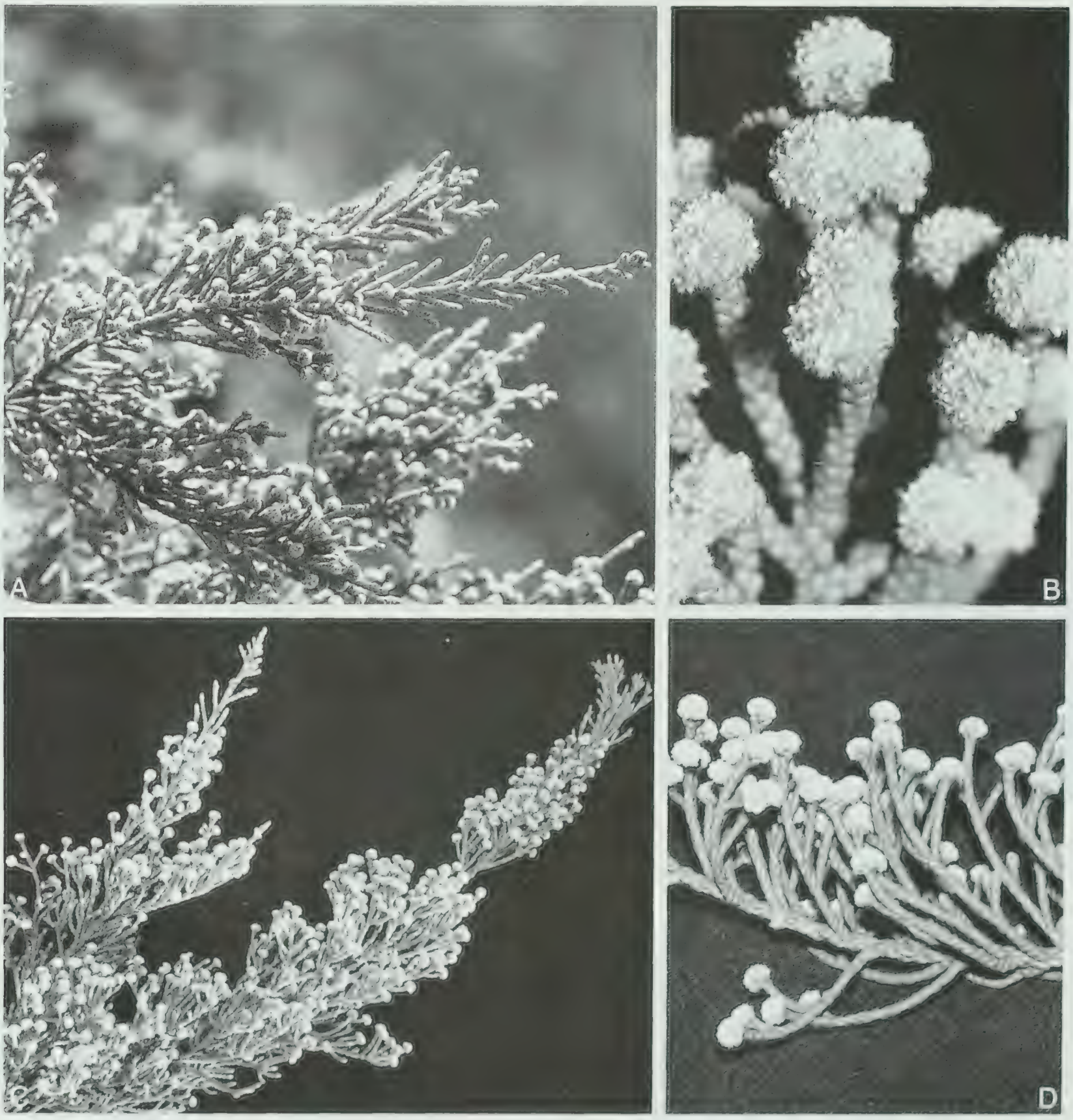


Figure 147 - **Raspalia microphylla**. *A, C, flowering shoot systems, B, inflorescences, D, arrangement of inflorescences.*

- *R. schlechteri* (fig. 154) has long, much-branched SGUs which may be subdivided into three parts. The proximal part bears determinate lateral shoots (dL) which end in a terminal inflorescence of 1st order (I) and several lateral inflorescences of branches of 2nd order (II). The medial part has the most promoted lateral shoots, these are mainly indeterminate, longer and more branched than the proximal shoots (iL). Besides the inflorescences of 2nd order of branches, they often bear additional inflorescences of 3rd order (III). Presumably their apices are able to grow on in the next season. The distal part of the SGU is characterized by usually branched vegetative lateral shoots (svL) which also appear at the tops of the indeterminate lateral shoots and occasionally among the flowering shoots. It is not known whether the apex of the SGU continues to grow on in the next season or dies off.

■ *R. trigyna* (fig. 155) is the only species of the family which is not distributed in the fynbos biome of the Cape Floral Kingdom but which is native to Natal-Kwazulu (fig. 1A: arrow). It differs from all remaining species of the genus in having the smallest inflorescences (2,5 mm in diameter) and leaves (1 mm long) (fig. 155C,D).

Like the other *Raspalia* species, *R. trigyna* is characterized by much-branched shoots and numerous inflorescences (fig. 155A). Fig. 155B illustrates the branching pattern of a two season old shoot system. The dominant shoot of the actual SGU (n) bears many densely packed sylleptic flowering lateral shoots (fig. 155B: sfL, fig. 155C). These are unbranched in the medial-distal zone and branched/determinate in the proximal zone, with inflorescences of 1st and 2nd order (fig. 155B: dL, I, II, fig. 155D). The lowermost lateral shoots repeat the branching pattern of the main axis, being indeteminate and covered with unbranched and branched flowering shoots.

The lateral flowering shoots lack any vegetative primordia, except for some uppermost lateral shoots which occasionally exhibit a renewal zone of 1st order below their terminal inflorescences (fig. 155B: rz'). As fig. 155B: n-1 shows, sympodially branched lateral shoot systems may arise from these renewal zones. The individual SGUs are connected in a monopodial manner (mc). The apices of the main axis and of the lowermost lateral shoots are able to continue their growth in the next season. They commence growth sylleptically so that the current SGU (n) becomes crowned by a vegetative top comprising several branched shoots of the next season's SGU (n+1) (fig. 155C). It is not known whether the leader shoot ends in a terminal inflorescence at any time or dies off in a vegetative condition. In the latter case the lowermost proximal shoots presumably continue the shoot system.

To demonstrate the diversity of flowering shoot systems seen in an individual species, a second flowering shoot system of *R. trigyna* is illustrated in fig. 156. Its regular sympodial branching pattern clearly differs from the shoot system described above. It may be interpreted as a five season old lateral shoot system, alternatively it may represent the senescent state of a plant or a shoot system under the influence of highly unusual habitat conditions.

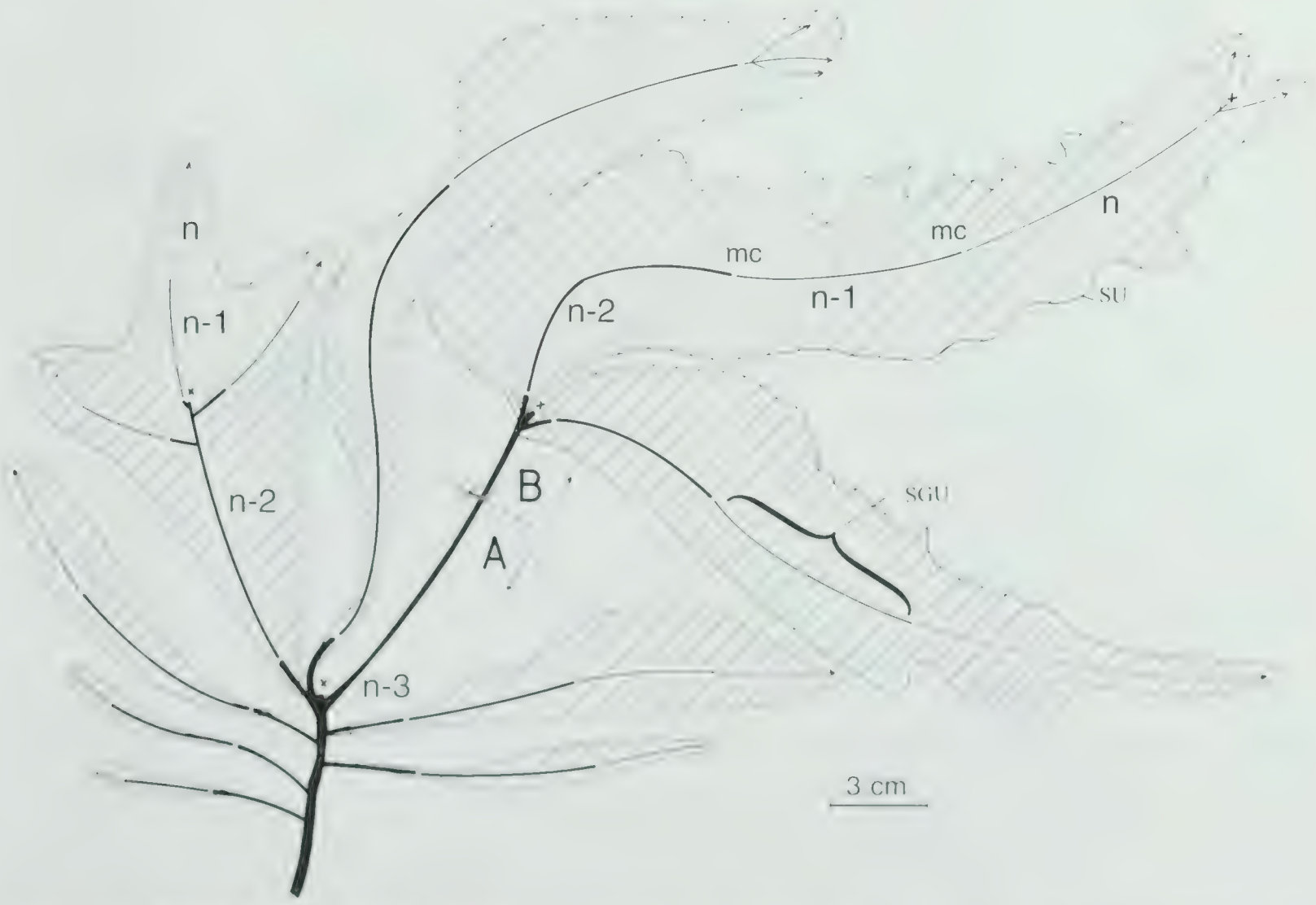


Figure 148 - **Raspalia microphylla**. *Scheme of a flowering shoot system.*
A: compare with fig. 149, B: compare with fig. 150.

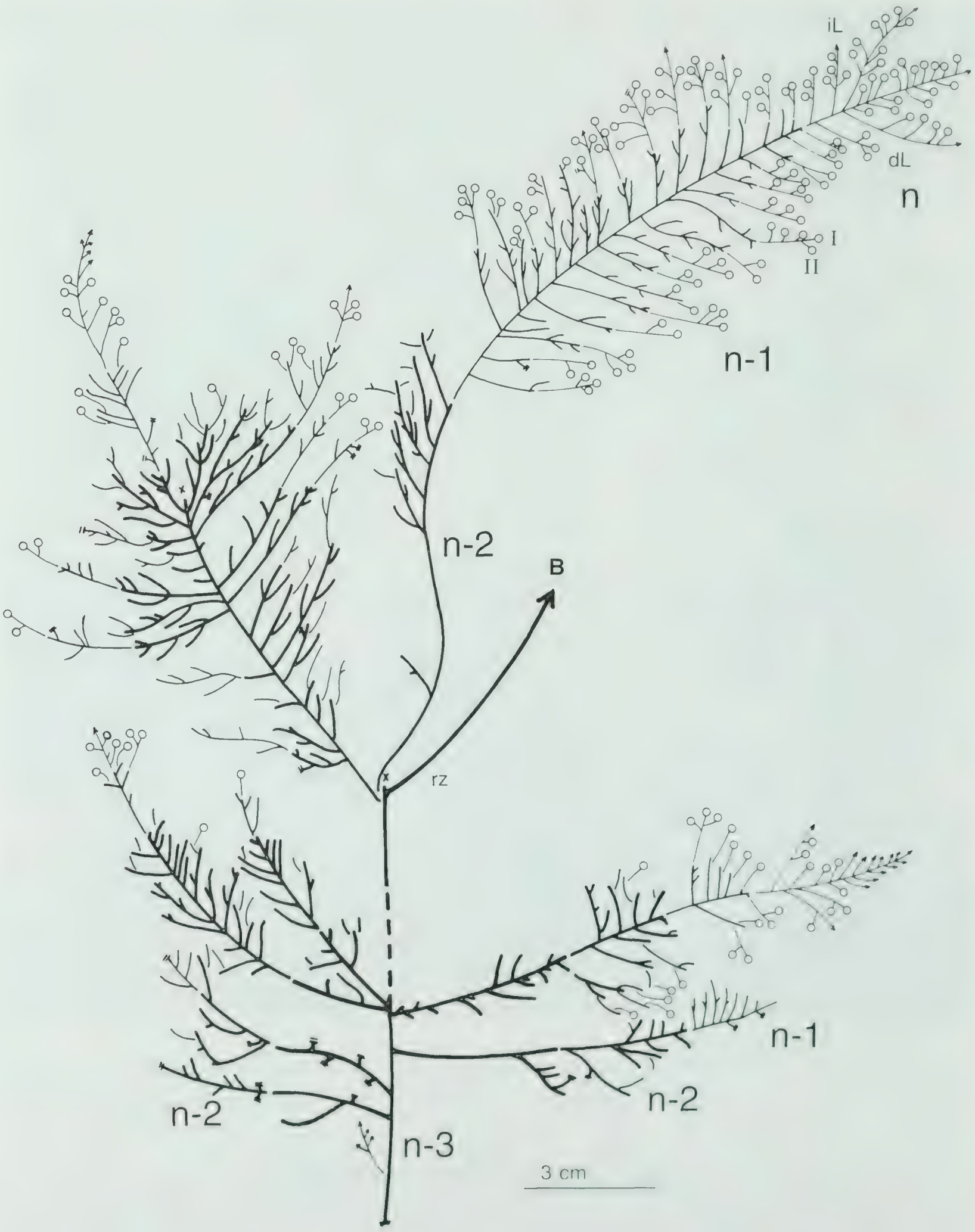


Figure 149 - **Raspalia microphylla**. *Profile of the shoot system marked as 'A' in fig. 148*

Figure 150 (p. 179) - **Raspalia microphylla**. *Profile of the shoot system marked as 'B' in fig. 148*

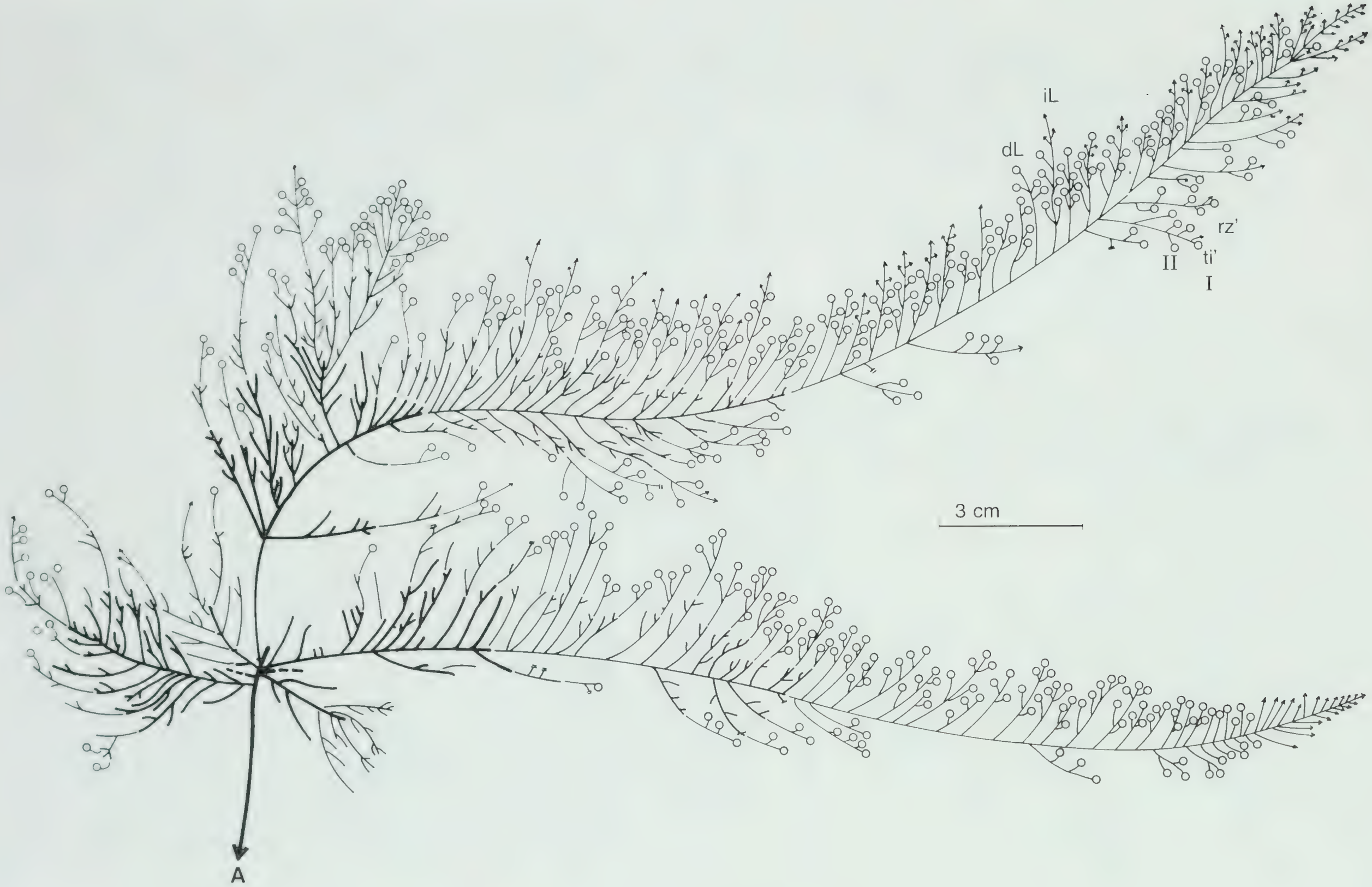

iL
dL
rz'
II
ti'
I
3 cm
A

Figure 151 - **Raspalia variabilis**. *Profile of a flowering shoot system.*

Leaf metamorphosis and inflorescence structure. Leaf metamorphosis is not very conspicuous in the genus (fig. 157). The upper leaves (2) are only slightly smaller, and the flower-subtending leaves (3) smaller and usually broader than the lower leaves (-2,-1,1). Independent of the presence of hairs on the lower leaves, the prophylls (4,5) and sepals (6) are always hirsute, *R. virgata* being the only exception (H).

The characteristically small inflorescences (two to seven millimetres in diameter) are aggregated in head-like clusters composed of five to twenty minute flowers (fig. 134B, 141E, 147B). Their apparently uniform habit masks the fact that the inflorescences in *Raspalia* species are more diverse in both organization and arrangement than are those of all other genera in Bruniaceae (fig. 158).

- In *R. globosa* (A), *R. microphylla* (B) and *R. trigyna* (C) the individual inflorescence is a cephaloid with a clearly precurrent terminal flower. In contrast, *R. stokoei* (E), *R. sacculata* (E), *R. villosa* (D) and *R. virgata* (F) are characterized by a clearly open apex. The inflorescence structure of the remaining species is not clear. The first reason is that sterile leaves may appear below the terminal flower as is shown in *R. trigyna* (C). The second reason is that the flowering sequence is highly variable as is shown in *R. microphylla* (B). Thus, in cases where the sterile top of the inflorescence axis is lacking and an acropetal flowering sequence is present simultaneously, it is not possible to distinguish whether the inflorescence is a cephaloid with a retarded development of the terminal flower, or a truncate cephaloid.
- The small globular inflorescences may comprise a single (A-C,E) or several individual (truncate) cephaloids (D,F). In *R. villosa* (D) lateral inflorescences with only a few flowers occasionally appear below the terminal inflorescence. In *R. virgata* the individual globular inflorescence may be a solitary truncate cephaloid (E) or a compound one (F) formed by several lateral truncate cephaloids, which latter may occasionally exhibit further branching. Vegetative primordia appear at the base of each individual part (F: rz'') and below the whole aggregate of flowering shoots (F: rz'). These suggest that the compound clusters may have originated from formerly solitary inflorescences, each with a renewal zone below. Both types, the simple and the compound inflorescence, are very similar in shape and size and thus the organization of the individual globose units is not directly recognizable. Compound inflorescences tend to occur in lateral positions while terminal inflorescences are always, as far as is known, solitary (truncate) cephaloids

Figure 152 - **Raspalia angulata**. *A, profile of a flowering shoot system, B, habit, and B', profile of the distal part of a flowering shoot system*

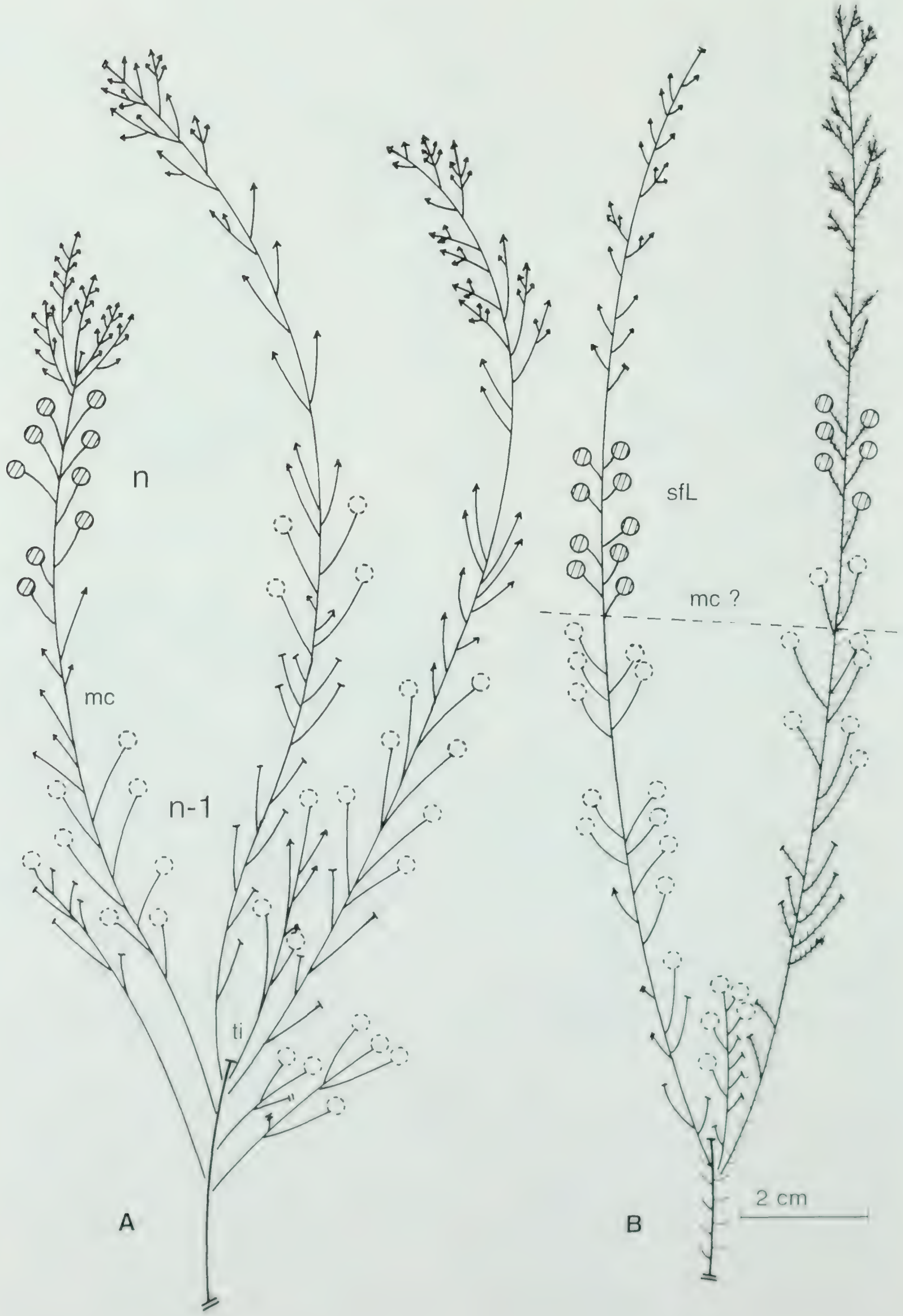


Figure 153 - **Raspalia phylicoides**. *Profiles of flowering shoot systems*

A

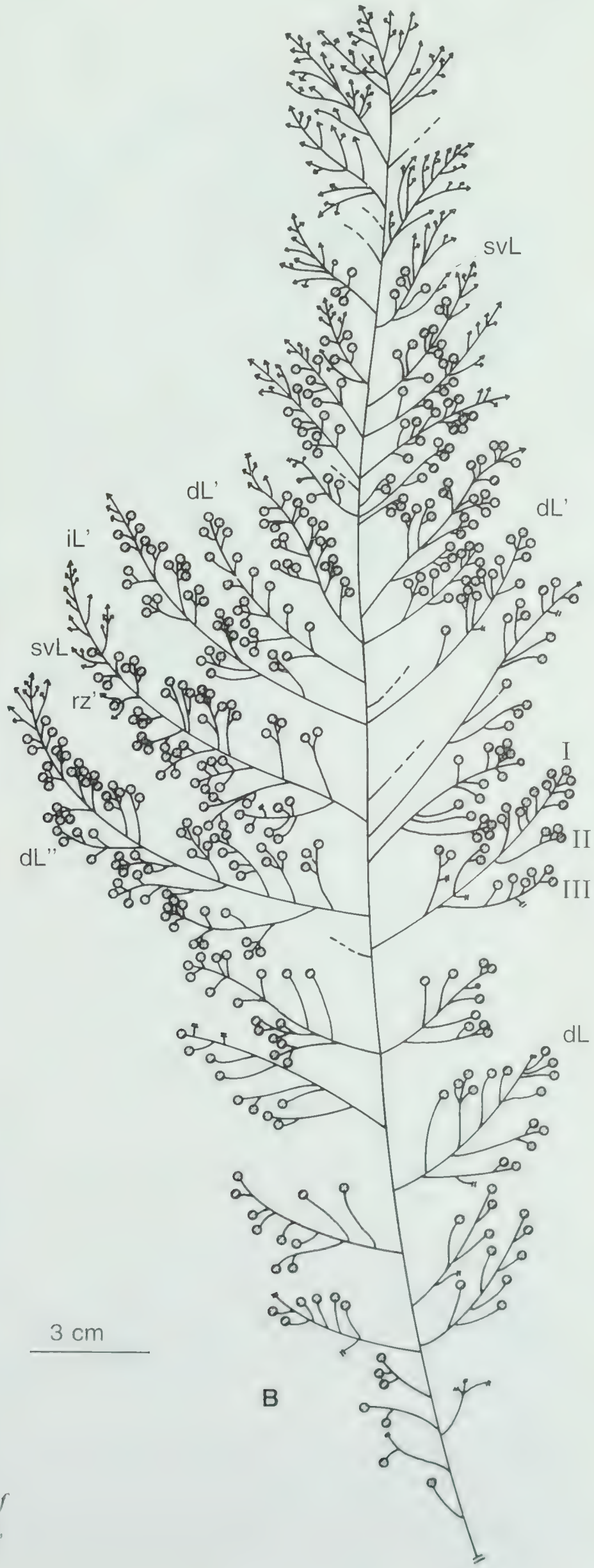


Figure 154 - **Raspalia schlechteri**. *A, habit of flowering shoot systems (Schlechter 1750, B), B, profile of the right shoot system in A.*

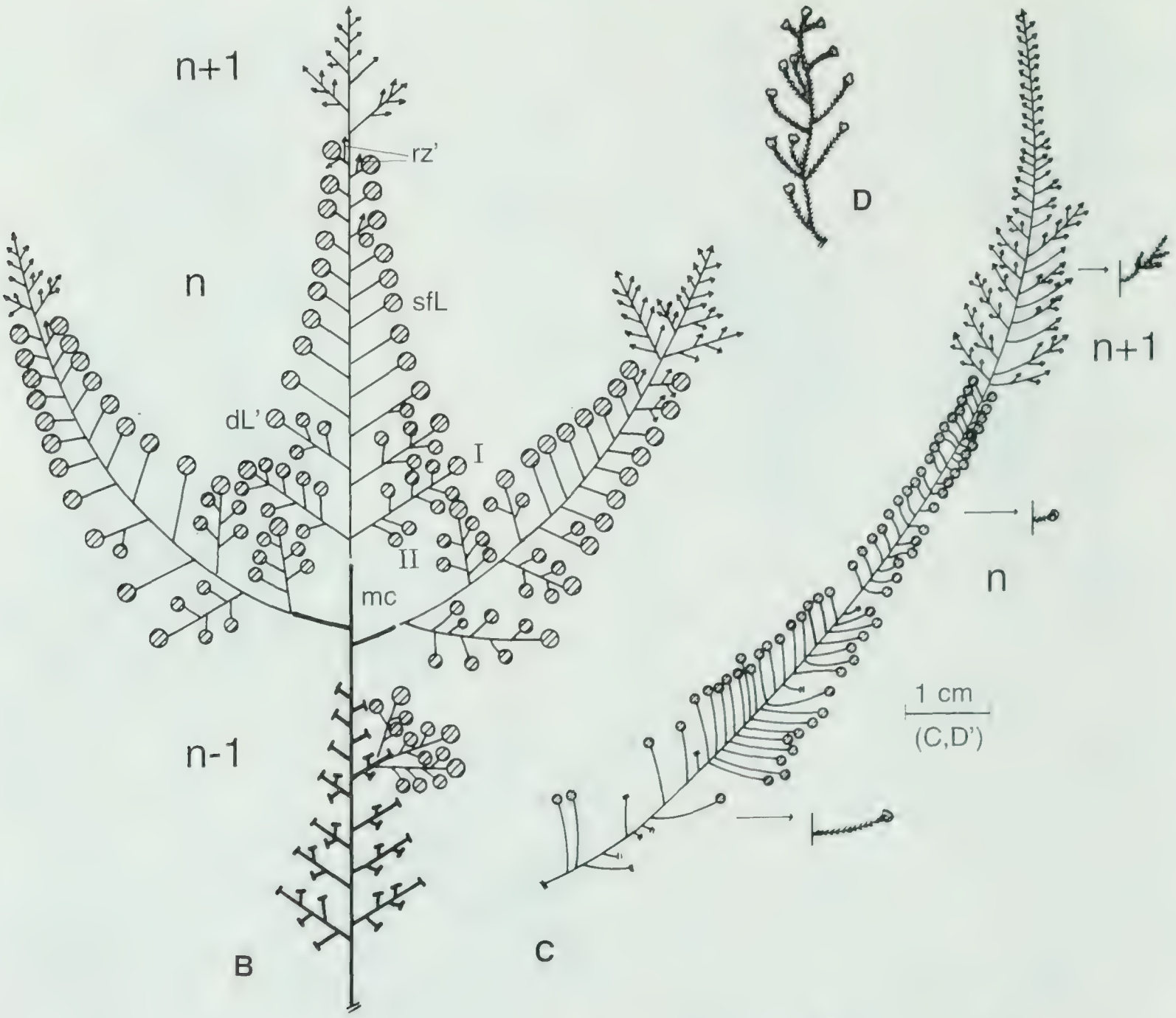


Figure 155 - **Raspalia trigyna**. *A, habit of flowering shoot systems (Taylor 2636, NBG), B, profile of a flowering shoot system, two seasons old, C, profile of the distal part of the right flowering shoot system in A, D, habit of a determinate lateral flowering shoot*

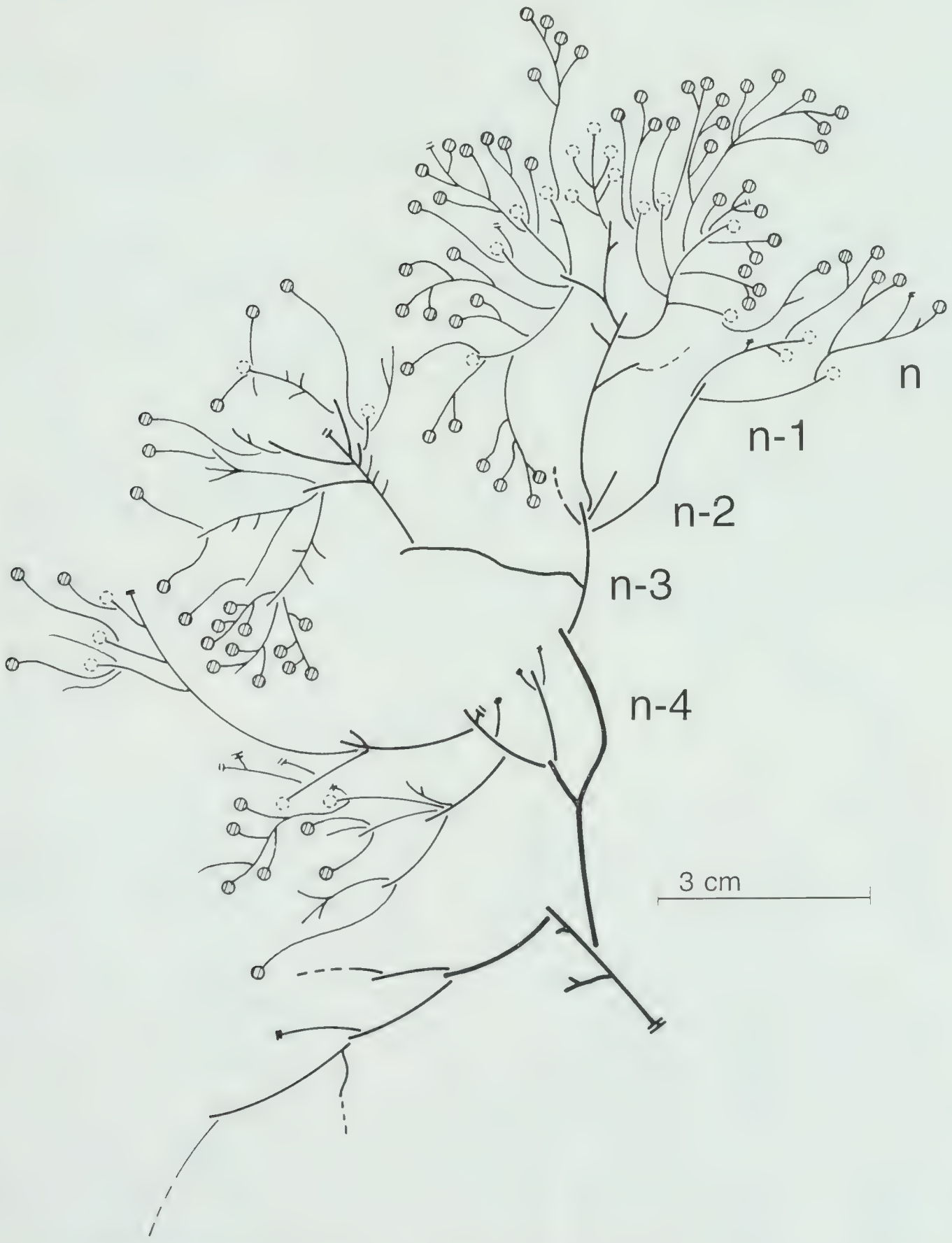


Figure 156 - **Raspalia trigyna**. *Profile of a flowering shoot system, six seasons old, showing extensive sympodial branching.*

Summary. The model of the genus is illustrated in fig. 159. The RS (A) is subdivided into a terminal, determinate inflorescence (ti), a subfloral renewal zone (rz) and a branching zone (bz) with sylleptically flowering lateral shoots (sfL). Those end in an inflorescence (I) and may be further branched (dL), bearing sylleptic vegetative lateral shoots (svL) and inflorescences of 2nd (II) and 3rd (III) order of branches.

As in other genera of Bruniaceae, the RS of *Raspalia* summarizes characteristic features of the genus and does not illustrate a particular species. In fact all *Raspalia* species studied differ in one or more aspects from the RS.

- *Raspalia* is the only genus in the family that demonstrates the conversion from a determinate into an indeterminate inflorescence, that is from a cephaloid into a truncate cephaloid (B: *7*).

- The terminal inflorescence may be absent. In this case, the SGUs concerned may be connected in a monopodial way (C: mc). The result is a dimorphism between flowering short-shoots and long leaders.
- As far as is known, the apex is able to grow on for about three seasons before dying off or forming a terminal inflorescence. Occasionally the apex starts to grow on sylleptically (D: *Tm*).
- The renewal zone usually has two to six cataleptic lateral shoots which may be of equal or unequal length (E). In the latter case the shoot system is overtopped by one long shoot (R+). Again a dimorphism results, but here based on sympodial branching.
- The branching zone varies in numerous ways (F). Both the sylleptic vegetative lateral shoots and flowering shoots of 1st, 2nd or 3rd order of branches may be absent. The lateral flowering shoots may be indeterminate and able to grow on in the next season (mc´). They may be equal or unequal in length and may appear along the whole SGU or only in the distal part. Finally they may be so densely aggregated that the globose inflorescences have a compound nature.

The species studied permit a subdividsion of the genus into two groups.

- Group I is characterized by (1) determinate inflorescences (cephaloids), (2) often lacking terminal inflorescences and (3) monopodial shoot connections, giving rise to sympodial units representing several seasons´ growth.
- Group II shows (1) truncate cephaloids (except *R. globosa*), (2) consistently terminal inflorescences and (3) a regular sympodial branching pattern, that is one season old sympodial units.

Figure 157 - ***Leaf metamorphosis in the genus*** **Raspalia**. *A*, R. globosa, *B*, R. sacculata, *C*, R. phylicoides, *D*, R. variabilis, *E*, R. villosa, *F*, R. staavioides, *G*, R. stokoei, *H*, R. virgata, *I*, R. angulata, *J*, R. schlechteri, *K*, R microphylla, *L*, R. trigyna.

-2,-1, 1: proximal leaves, 2: distal leaves, 3: flower-subtending bract, 4,5: prophylls, 6: sepal

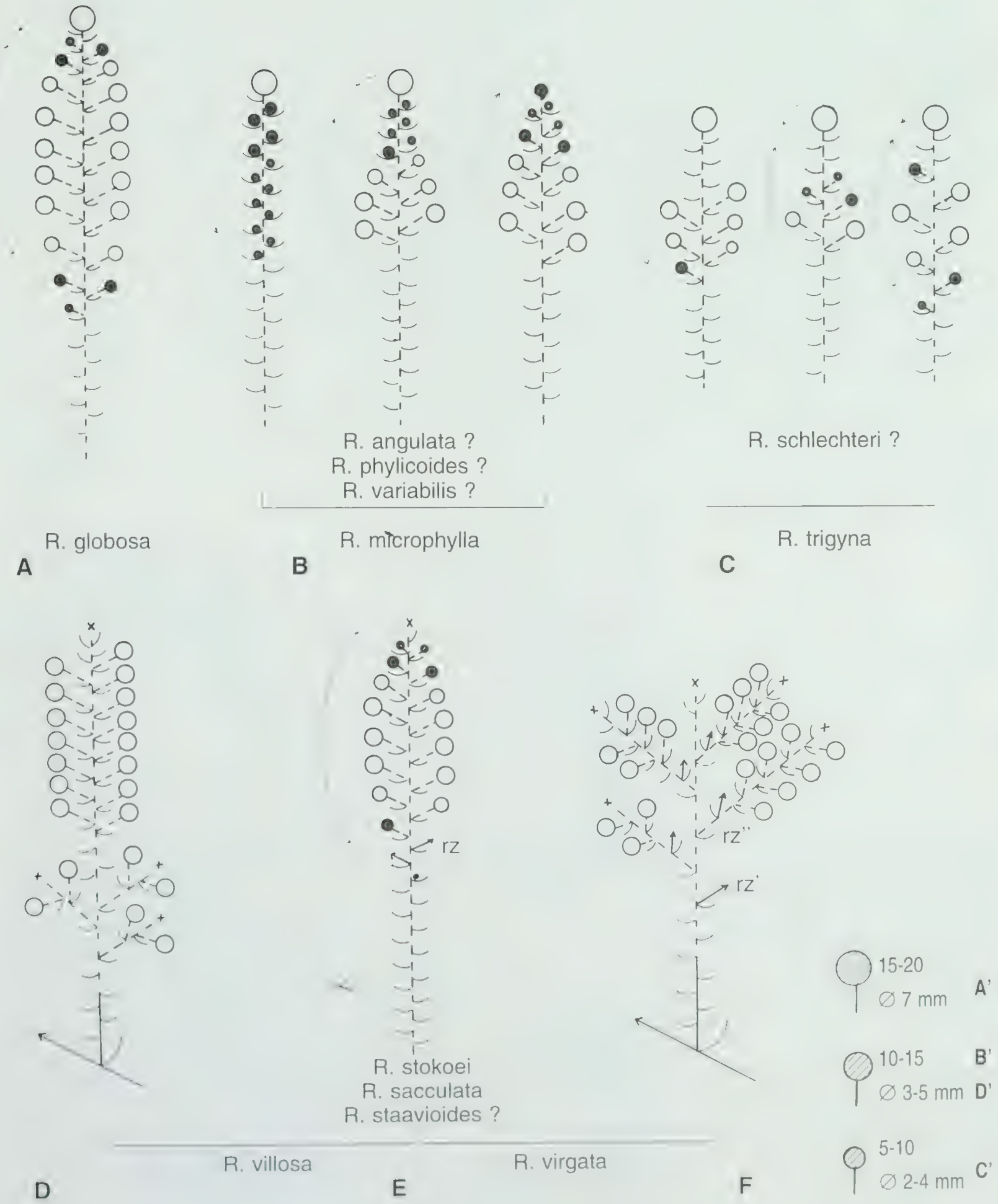


*Figure 158 - **Inflorescences in the genus* **Raspalia**. *A-F, profiles, A'-C',E' form, size and flower number of the inflorescences. Arrows: flowering sequence.*

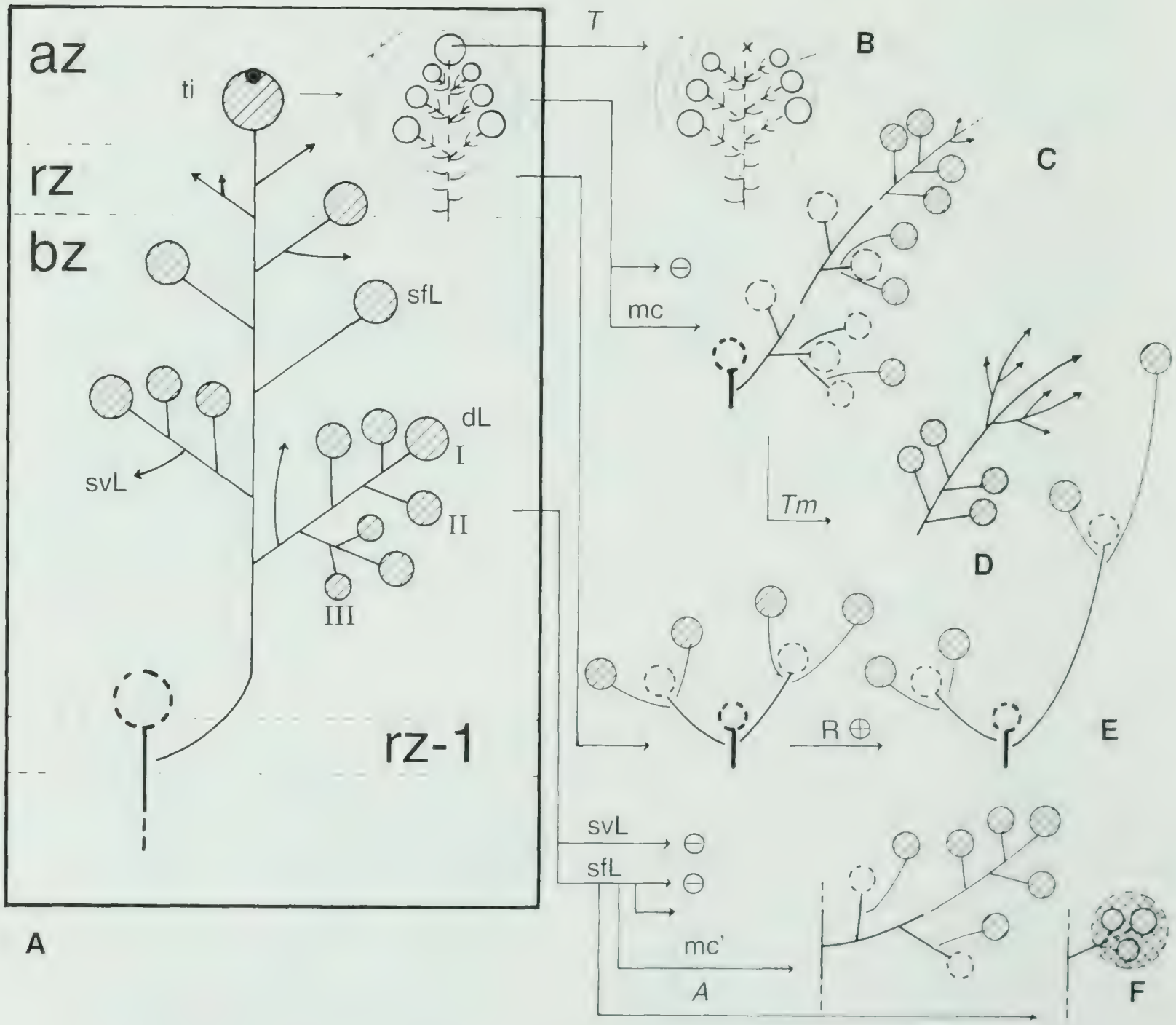


*Figure 159 - **Model of the genus* Raspalia*.** A, reference system (RS) showing the terminal inflorescence, the renewal zone below and the branching zone with vegetative and flowering lateral shoots. B-F, variations concerning the truncation of the individual inflorescence (B), the lack of the terminal inflorescence and the monopodial connection of SGUs (C), the precurrent development of the next season's shoots (D), the unequal promotion of the renewal shoots (E), and the presence of indeterminate lateral shoots and of compound inflorescences (F). A, aggregation, T, truncation, Tm, shifting in time.*

3.10 ***Staavia*** Dahl

St. dodii *and* S. glutinosa, *characterized by conspicuous capitate inflorescences, are the most attractive members of the family. Both species and* St. radiata *were studied in their natural habitats.*

S. dodii *is known only from fourteen populations in the Cape Peninsula Nature Reserve (Moll & Gubb 1981:3). The shrubs are found at windy locations between rocks within a coastal fynbos community (fig. 3A, 159A).*

S. glutinosa *was studied at a locality on Table Mountain (fig. 162A) where thick clouds provide humidity (fig. 2D). A population of at least fifteen plants of about one meter in height was found within a dense mountain fynbos community.*

S. radiata *is one of the more common species of the Bruniaceae and distributed in a large area of the Western Cape. It was studied at Karbonkelberg (Cape Peninsula, fig. 2B) and at Soetanysberg (near Bredasdorp). The shrubs were about 50 cm in height and formed the understory of a rich Proteoid fynbos community.*

Cuttings of S. dodii, S. glutinosa, S. radiata *and* S. dregeana *(fig. 169A,B) were studied in the nursery of the National Botanic Garden Kirstenbosch. Because of the horticultural value of some* Staavias, *a project has been undertaken at the nursery to cultivate them. In preliminary germination trials, treatments using concentrated sulphuric acid and gibberellic acid were successful for* S. dodii *(Wolff 1990).*

S. capitella, S. verticillata *and* S. zeyheri *have been analyzed from herbarium material.*

Figure 159 - **Staavia dodii**. *A, locality at Olifantsbos, Cape Peninsula Nature Reserve, B, characteristic growth form of a shrub.*

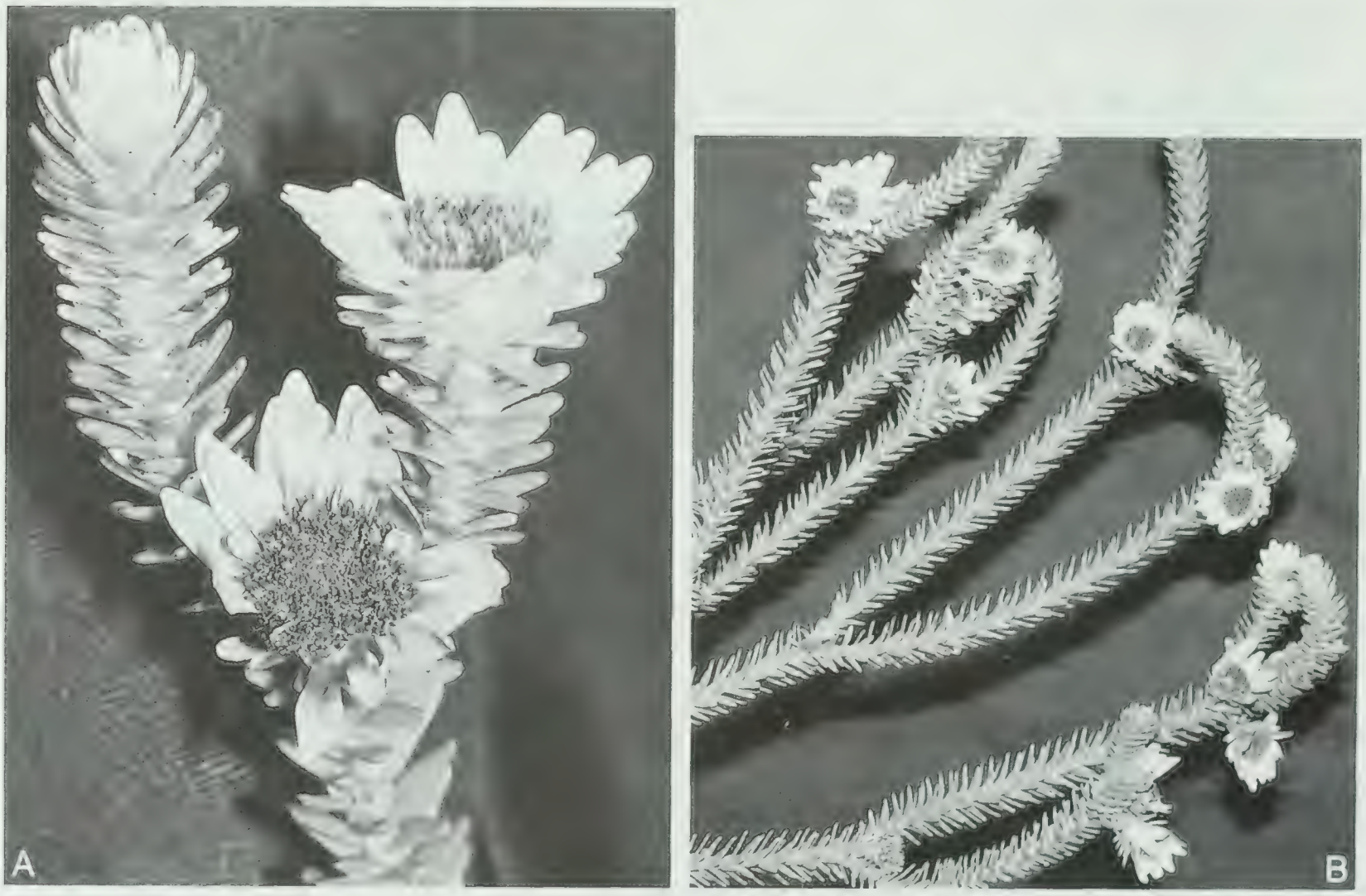


Figure 160 - **Staavia dodii**. *A, a flowering shoot system, two seasons old. Note the position of the renewal zone below the terminal inflorescence, the different developmental stage of the two renewal shoots and the formation of flower-like inflorescences. B, habit of a flowering shoot system, four seasons old (compare with fig. 161A).*

Growth and branching pattern. Four of the ten recognised species of the genus are rare or endangered, two being probably extinct (Moll & Gubb 1981, Hilton-Taylor 1996). The ecological study made by Moll & Gubb (1981) suggested in the case of *S. dodii* that harvesting, too frequent fires and the aggressive expansion of Australian invaders (e.g. *Acacia cyclops*) have contributed to the decline of the populations.

According to Moll & Gubb (1981) *S. dodii* is an obligate reseeder, germinating after fire. The seedling passes a juvenile, purely vegetative phase of five to eight years during which the apex of the unbranched primary shoot continues to grow on. The forming of the first terminal inflorescence causes the sympodial branching pattern which characterizes the growth form of the shrub (fig. 159B).

Moll & Gubb (1981) compared the branching pattern and flowering behaviour of three plants of different life ages that is of eight, twelve and twenty-five seasons (fig. 161D). They were able to show that with increasing age, the length of the SGUs and the number of florets per inflorescence decrease (from forty to twenty) and that the leaves are shed earlier (after two or three seasons instead of after four or five). The number of renewal shoots increases in the early reproductive seasons up to a maximum of six, which is achieved in ten to twelve season old shrubs. After 23-25 seasons the shrubs start to become senescent, usually forming only one renewal shoot. After about 30 seasons the shrubs die off. The phenology of the three plants studied differs only slightly (fig. 161D). (The period of vegetative growth lasts from June/July until March, and that of flowering from December until July/August.)

The branching behaviour of *S. dodii* as observed in the present study is illustrated in fig. 161A-C. These observations were made at the end of October 1987 at Olifantsbos, on an 80 cm high plant of about fifteen seasons in age (fig. 3A). Following the phenology cited (Moll & Gubb, 1981, fig. 161D), the shrub was mid-vegetative phase, showing the first inflorescences. As regards the number of renewal shoots per SGU (one to four), the number of florets per inflorescence (twenty to thirty) and the persistence of the leaves (about three seasons) the findings of this study agree with those of Moll &

Gubb (1981). However, the latter authors made no mention of the occasional presence of one or two sylleptic flowering lateral short-shoots below the terminal inflorescence (fig. 161A: sfL). These lateral inflorescences develop later than the terminal one and may still beat the flowering stage when the terminal inflorescence has reached the stage of capsule dehiscence (fig. 176B,C). Anthesis of the lateral inflorescences lasts until October (and not until August) when in contrast to the findings of Moll & Gubb (1981), the first inflorescences of the next season have already started to flower (fig. 161A: cfR).

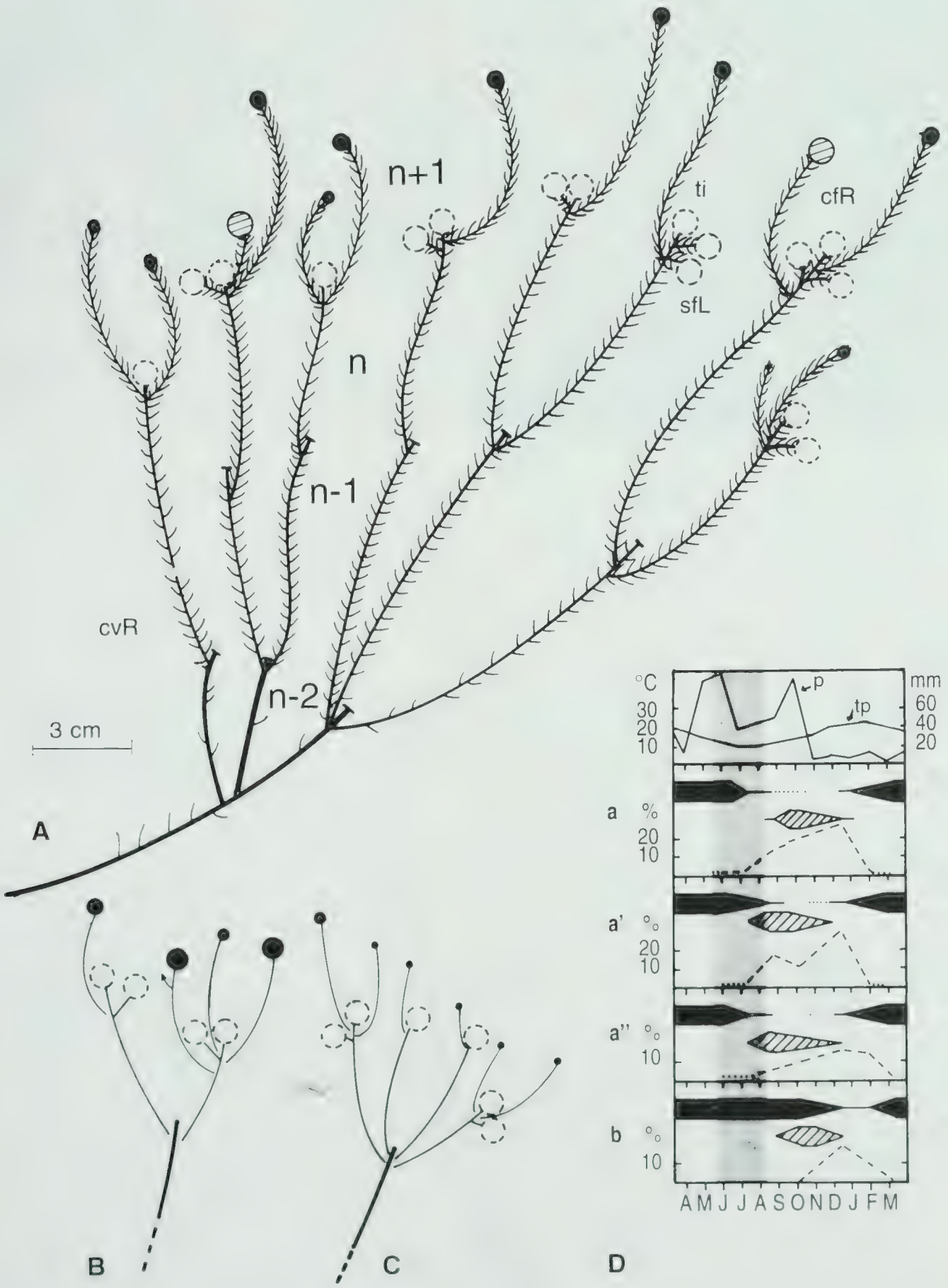


Figure 161 - **Staavia dodii**. *A-C, profiles of flowering shoot systems (compare A with fig. 160B), D, phenology of* S. dodii *(a, eight, a', twelve, a'', twenty-five seasons old) and* S. radiata *(b) compared with temperature (Tp) and precipitation (p) (after Moll & Gubb 1981).* cvR, *cataleptic vegetative renewal shoot. The black areas in D represent the time of anthesis, the hatched areas the time of seed-dispersal; the dotted lines show the duration and quantity (in %) of vegetative growth (the two peaks in a' are caused by feeding insects)*

Figure 162 - **Staavia glutinosa**. *A, locality on the south eastern slope of Table Mountain, Kirstenbosch (above Nursery Ravine), B, close-up of the attractive flower-like inflorescences.*

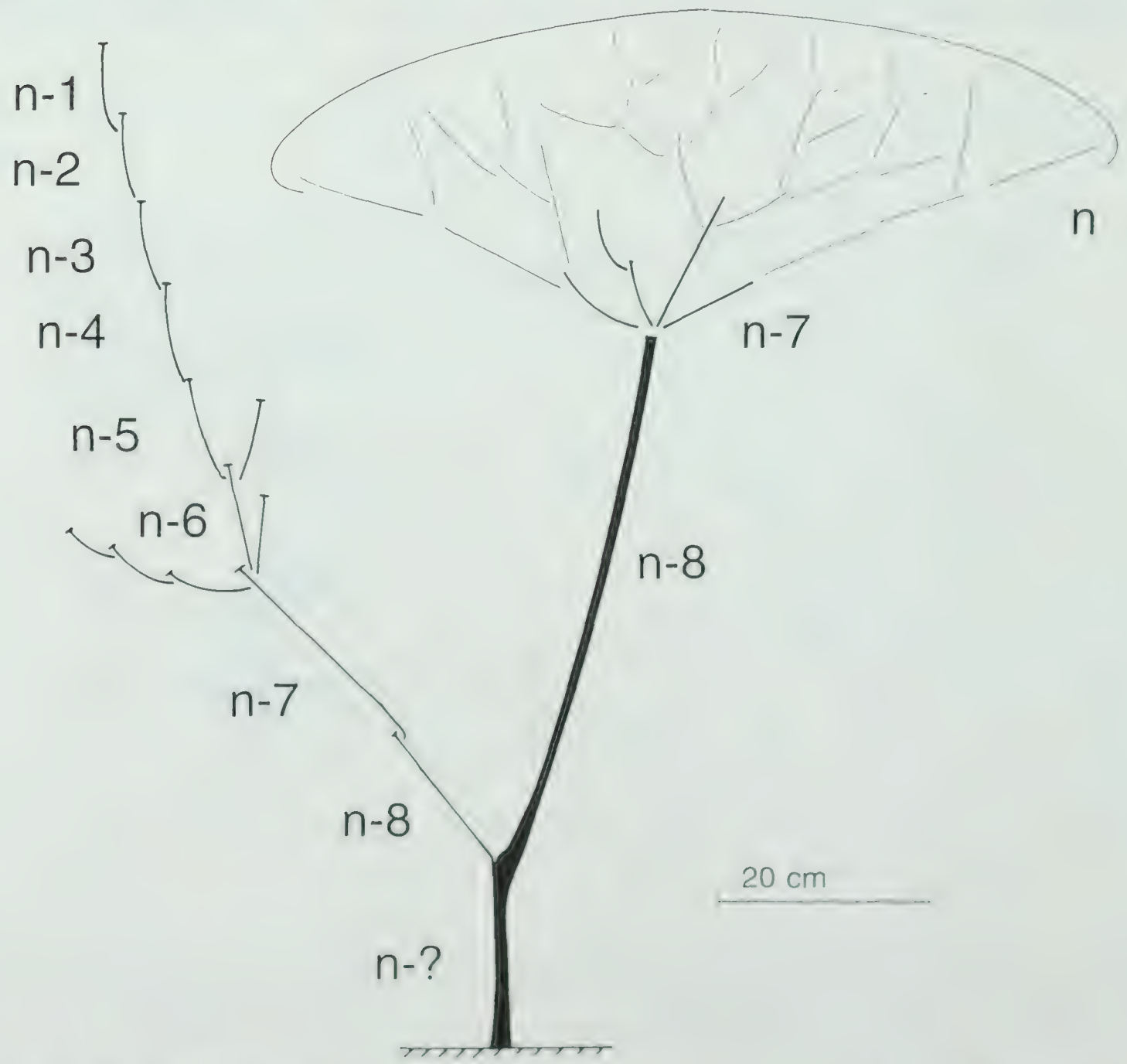


Figure 163 - **Staavia glutinosa**. *Growth form of a plant growing above Nursery Ravine, Kirstenbosch, one meter in height and at least ten seasons old.*

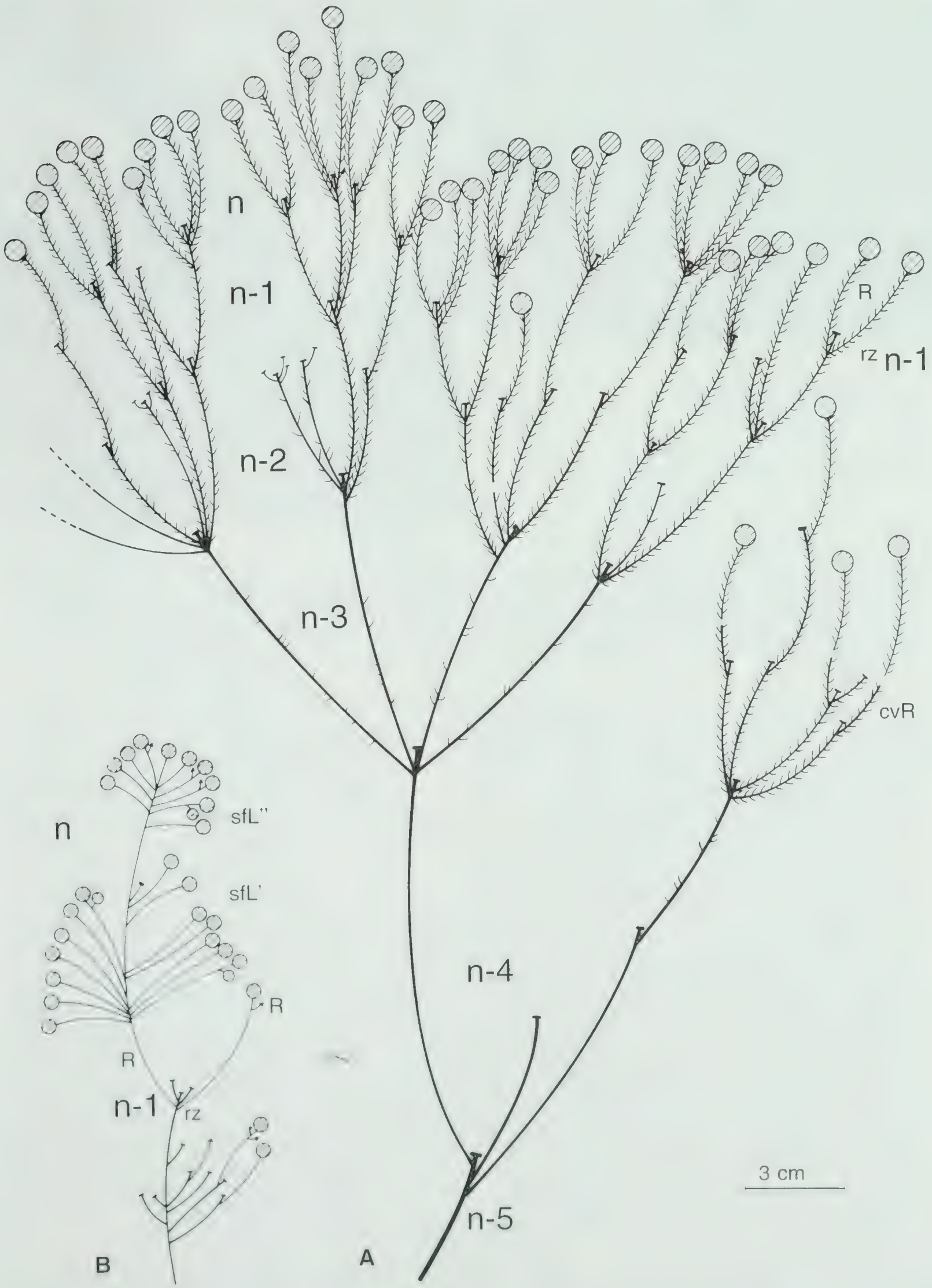


Figure 164 - **Staavia glutinosa**. *A, B, profiles of flowering shoot systems, six (A) and two seasons old (B). Note the different branching pattern with terminal inflorescences only in A and with numerous additional sylleptic flowering lateral shoots (*sfL*) in B.* cvR, *cataleptic vegetative renewal shoot; compare with fig. 165.*

Figure 165 - **Staavia glutinosa**.
Flowering shoot systems,
A, with terminal inflorescences only,
B, with additional sylleptic flowering lateral shoots.
Compare with fig. 164.

As a consequence the assigning of a particular inflorescence to the previous or current SGU may only be achieved by close observations of the stage of anthesis (compare fig. 176A-C). In conclusion it may be said that the *S. dodii* specimen observed during October 1987 was phenologically more similar to *S. radiata* in flowering throughout the year, than to *S. dodii* as described by Moll & Gubb (1981).

The branching pattern and flowering behaviour of *S. glutinosa*, *S. radiata*, *S. capitella* and *S. dregeana* agree largely with that of *S. dodii*. However, the following data were gathered from plants of unknown age and thus reflect only one aspect of the variability possibly present in the species.

- The profiles of *S. glutinosa* as shown in fig. 163, 164 and 166 illustrate the regular sympodial branching pattern of the plants. The length of individual SGUs decreases with age. An extreme case is shown in fig. 163 where the appearance of a stem bearing an umbellate canopy results from SGUs of remarkably different length. Each SGU has three to four (one to six) cataleptic renewal shoots (R) below the terminal inflorescence, these mimic the mother axis in growing out and flowering in the following season. As in *S. dodii* (fig. 161A: cvR), weaker renewal shoots may remain vegetative for one season (fig. 164A: cvR) and flower in the next season. The shrubs studied clearly differ in the length of the SGUs and in the number of sylleptic flowering lateral shoots. Fig. 164A and 165A show a plant of which individual SGUs are short (three to six centimetres in length) and almost unbranched, while other plants (fig. 164B, 165B, 166A,B: sfL) have long (about ten centimetres in length) SGUs bearing numerous sylleptic flowering lateral shoots arranged both below the renewal zone and in the central region of the SGU concerned. As all plants studied are from the same slope on Table Mountain, it is presumed that they are of the same age. Thus, the differences are not explicable in terms of life age as it was for *S. dodii* (Moll & Gubb 1981). In comparison with *S. dodii*, the lateral shoots of *S. glutinosa* are much longer and may be branched, bearing inflorescences of 2nd order of branches (fig. 164B: sfL''). As fig. 166A shows renewal zones of 1st order of branches may appear below the uppermost lateral inflorescences (rz')

S. radiata, *S. dregeana* and *S. capitella* (fig. 172, 173A) resemble each other closely in inflorescence morphology. Their appearance is attributable to the clear sympodial branching pattern, with one to four renewal shoots per SGU. Usually the SGUs are shorter and the inflorescences smaller and less conspicous than in *S. dodii* and *S. glutinosa*

- *S. radiata* (fig. 167, 168, 173B) was studied at two different localities. Fig. 167A illustrates a ten season old flowering shoot system of a plant from the Karbonkelberg. The pattern is regular and the

length of individual SGUs about five centimetres. The second specimen (fig. 167B) originated from the Soetanysberg near Bredasdorp. The SGUs were slender and up to ten centimetres in length. Lateral flowering short-shoots were often present and tended to have renewal zones and renewal shoots of 1st order of branches (rz´, R´). It is not known whether these differences are the result of different habitat conditions or plant ages or whether they merely represent normal variability between different populations of a species.

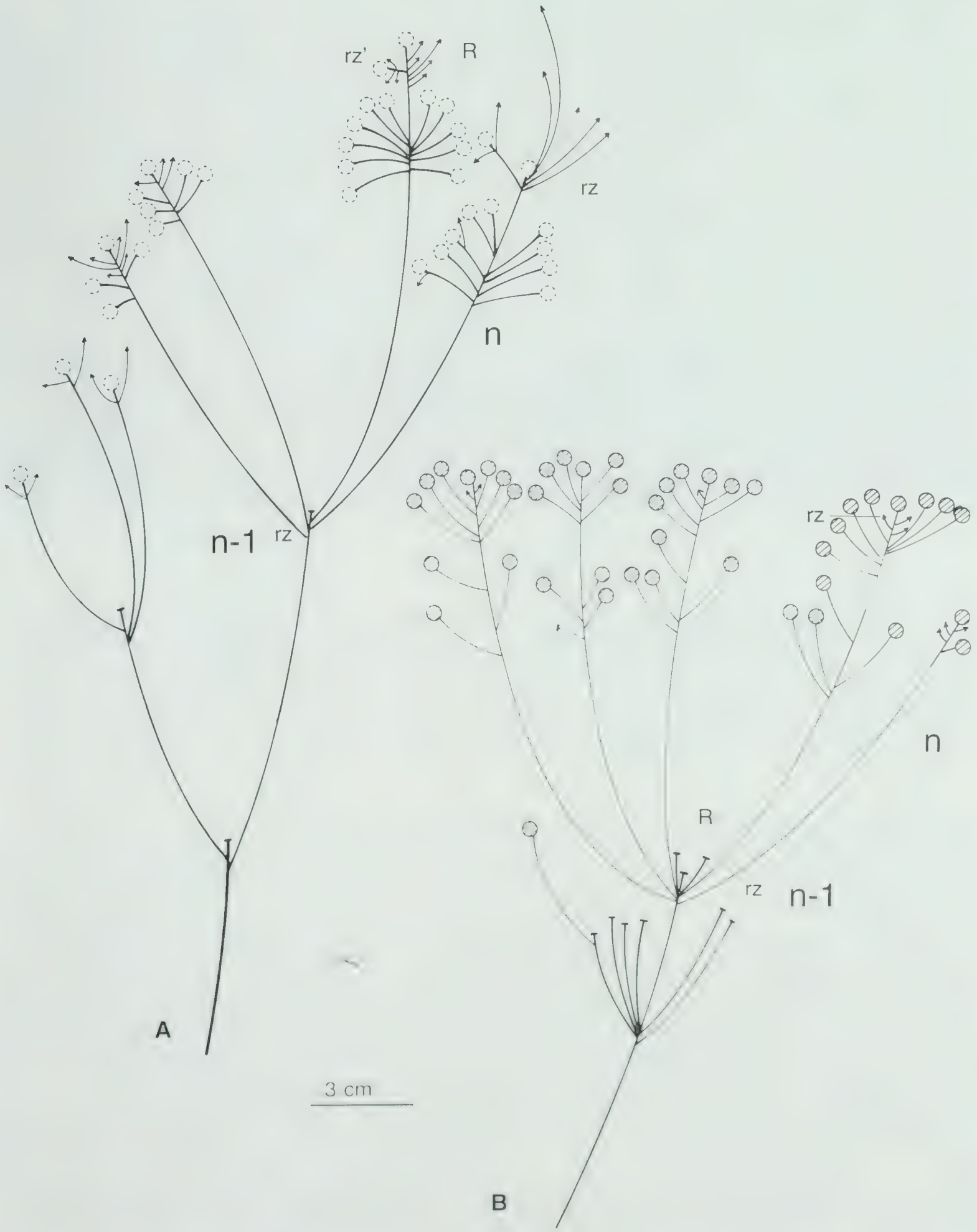


Figure 166 - **Staavia glutinosa**. *Profiles of a postfloral (A) and a flowering (B) shoot system. Note the position of the renewal zone (rz) below the terminal inflorescence and the occasional presence of a renewal zone of 1st order (rz') below the uppermost lateral inflorescence.*

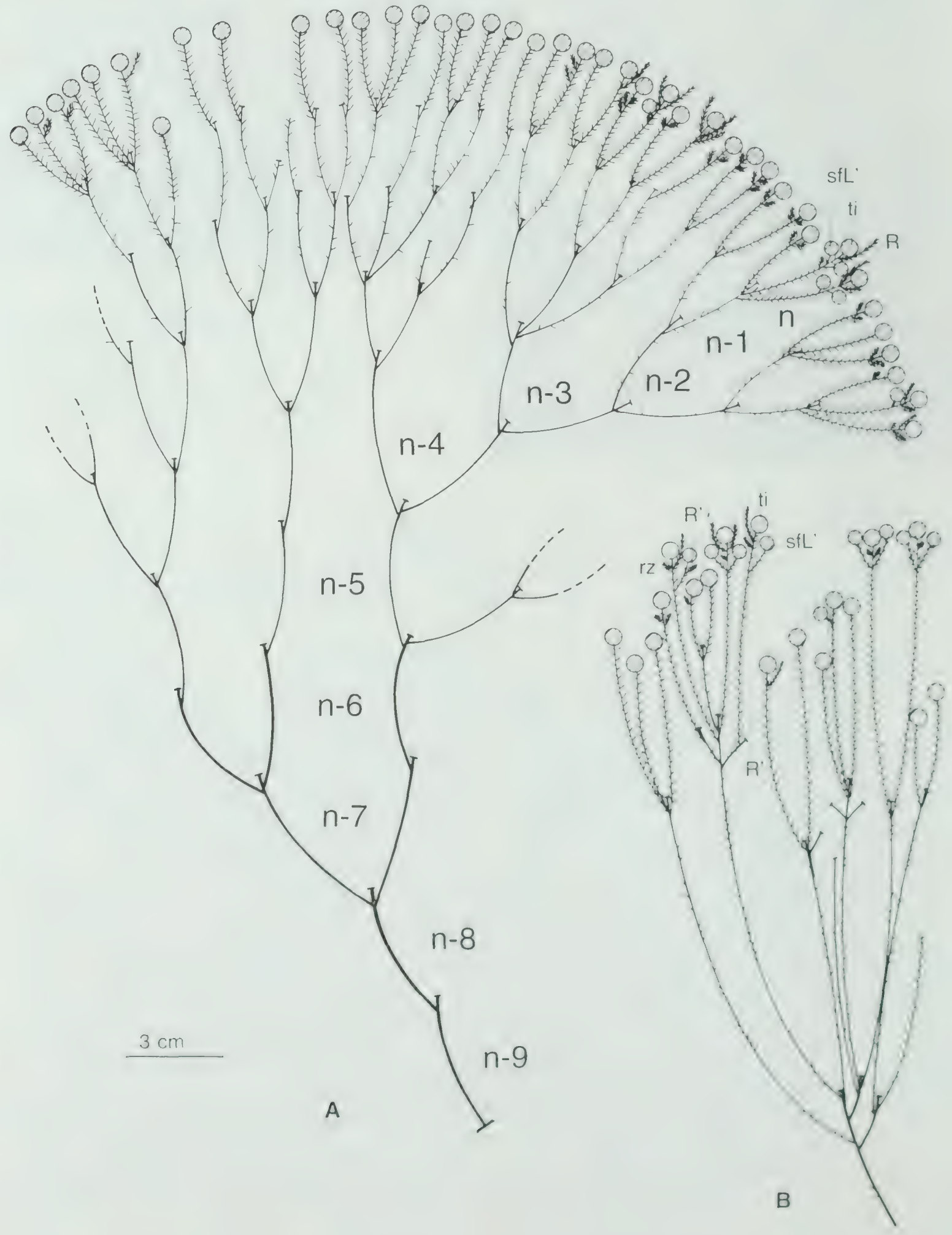


Figure 167 - **Staavia radiata**. *A, B, profiles of flowering shoot systems, ten (A) and three (B) seasons old. Note the different lengths of the SGUs (A: about 5 cm, from a locality at Karbonkelberg; B: about 10 cm, from a locality at Soetanysberg)*

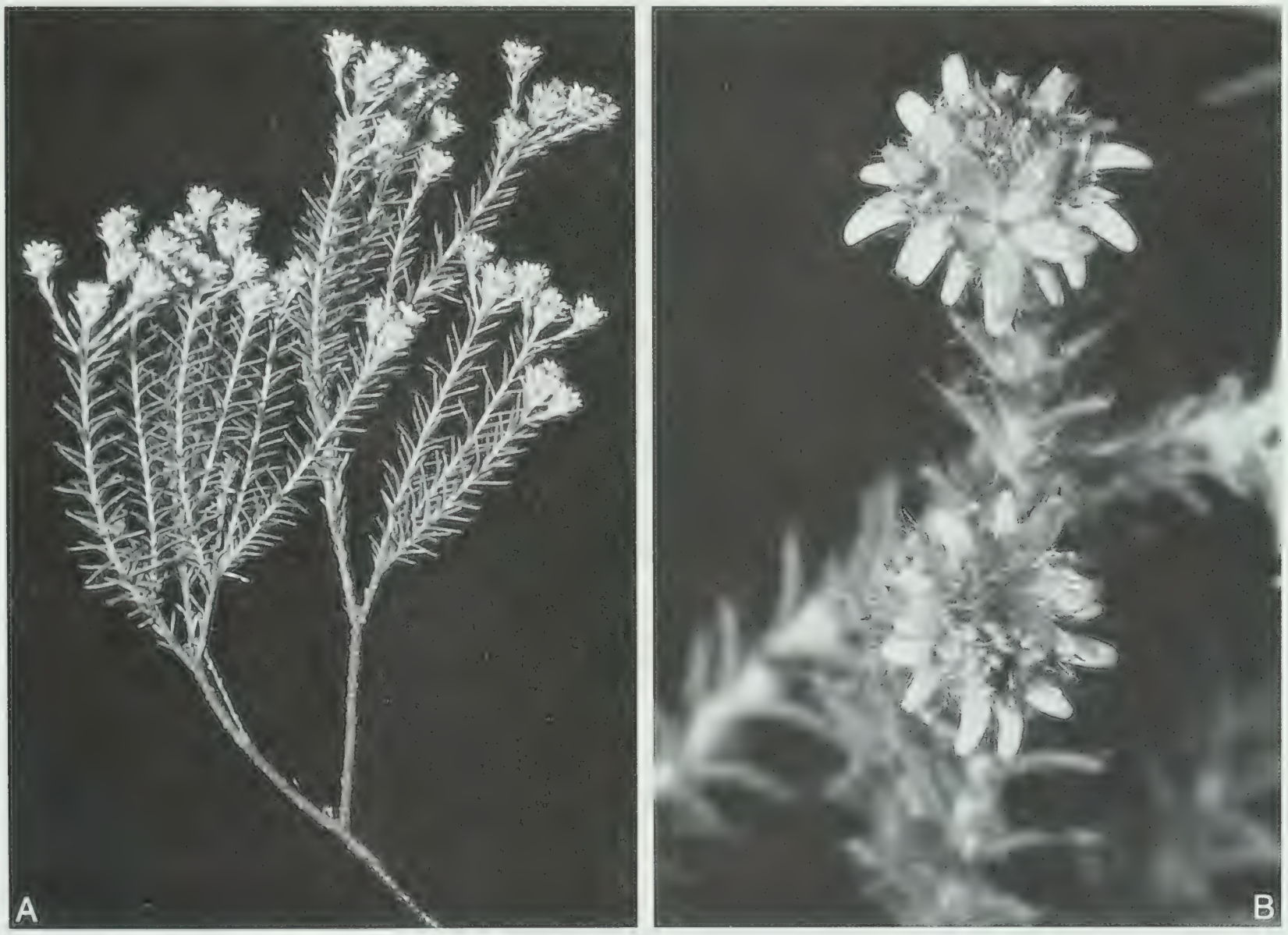


Figure 168 - **Staavia radiata**. *A, flowering shoot system, four seasons old, B, inflorescences.*

- *S. dregeana* is cultivated at the nursery of the National Botanic Garden Kirstenbosch, where seven potted cuttings from two different localities were available for morpohological study (fig. 169A,B). In comparison with the regular sympodially branched shoot system noted in herbarium specimens (fig. 171) the cuttings bore much shorter and more branched SGUs (fig. 170A) and occasionally also new proximal shoots (fig. 169D, 170B). These unusual branching patterns may have been artificially induced by the propagation process.

S. zeyheri (fig. 173C, 174) also has a sympodial branching pattern, but differs from all other species of the genus in having compound inflorescence aggregates. Usually eight to twelve individual inflorescences are densely crowded at the top of the main axis of the SGU, forming a head-like cluster. This is composed of a terminal inflorescence and sylleptic flowering lateral short-shoots of 1st order of branches (fig 174B: ti, sfL'). Occasionally very large inflorescence aggregates appear with up to 45 individual inflorescences and determinate lateral shoots with additional inflorescences of 2nd order of branches (fig. 174B: dL, II). Though the terminal cluster of inflorescences resembles the compound inflorescences found in *Nebelia* (fig. 100) the two genera differ in the position of the renewal zone. In *S. zeyheri* the renewal shoots appear below the terminal individual inflorescence (fig. 174B: rz) and not (as in *Nebelia)* below the whole inflorescence aggregate (fig. 118C). Thus, relative to the position of the renewal zone *S. zeyheri* agrees with other species of the genus regardless of the appearance of the inflorescence aggregates.

In contrast to the species described above which are all characterized by a terminal inflorescence and a regular sympodial branching pattern, *S. verticillata* (fig. 173D, 175) demonstrates a monopodial connection of the SGUs (mc). The apex of the dominant shoot remains open for at least two seasons before the shoot system changes to sympodial branching. It is not clear whether it always ends in an in-

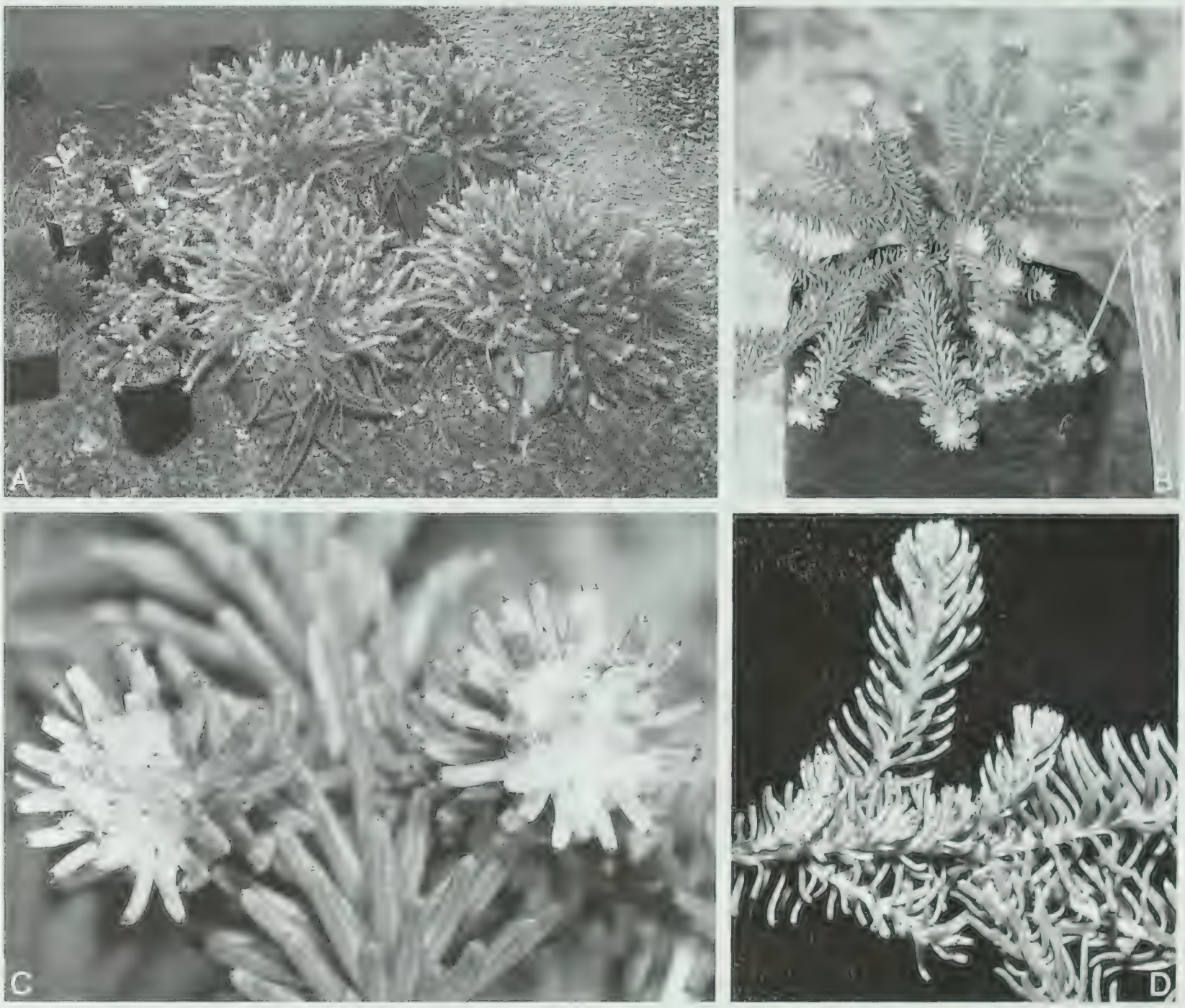


Figure 169 - **Staavia dregeana**. *A, B, potted plants at the nursery of the National Botanic Garden Kirstenbosch, C, inflorescences, D, new shoots forming at the base of the SGU.*

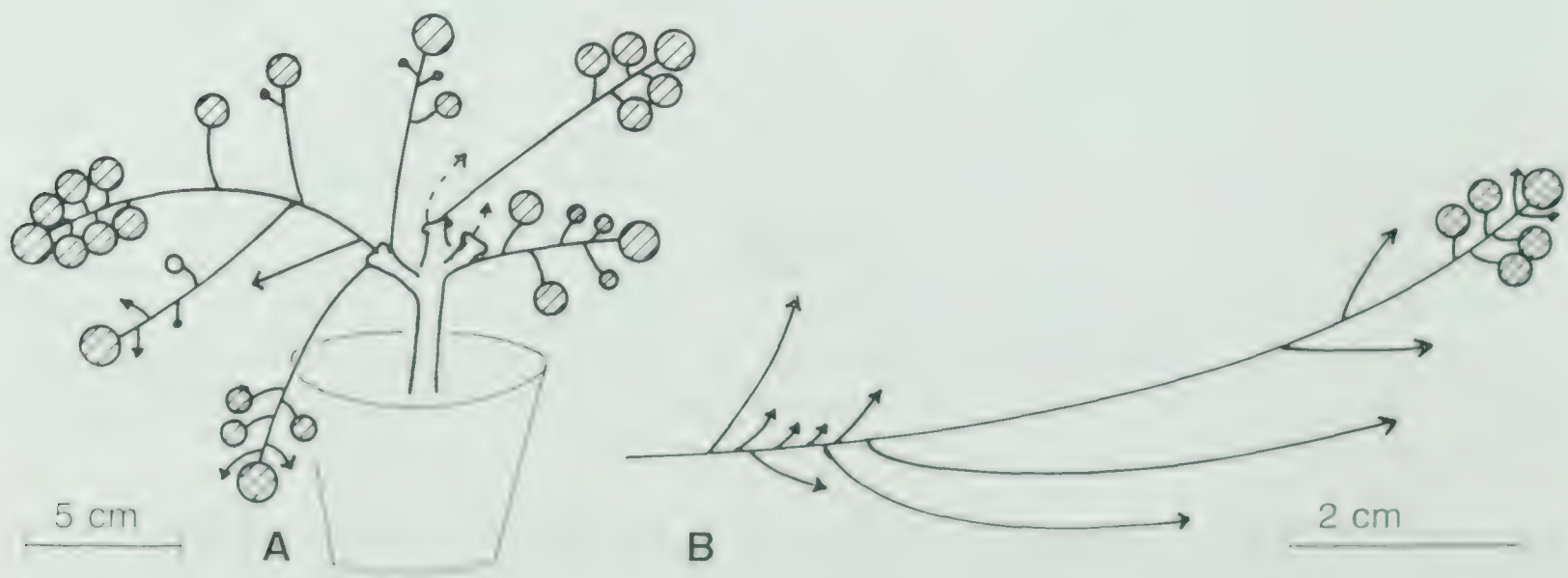


Figure 170 - **Staavia dregeana**. *A, profile of a potted plant, B, profile of a shoot with sprouts in the proximal region*

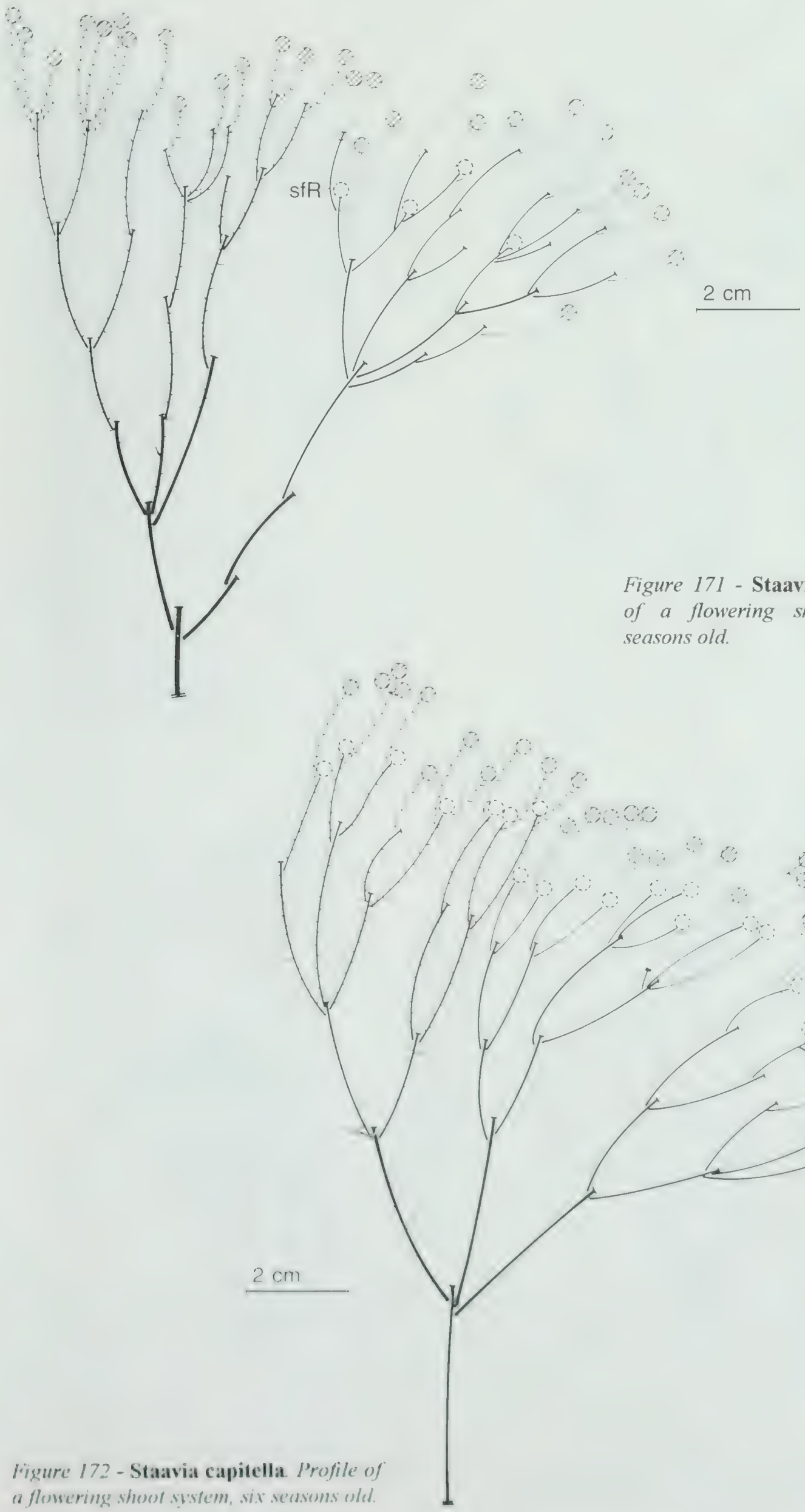


Figure 171 - **Staavia dregeana**. *Profile of a flowering shoot system, seven seasons old.*

Figure 172 - **Staavia capitella**. *Profile of a flowering shoot system, six seasons old.*

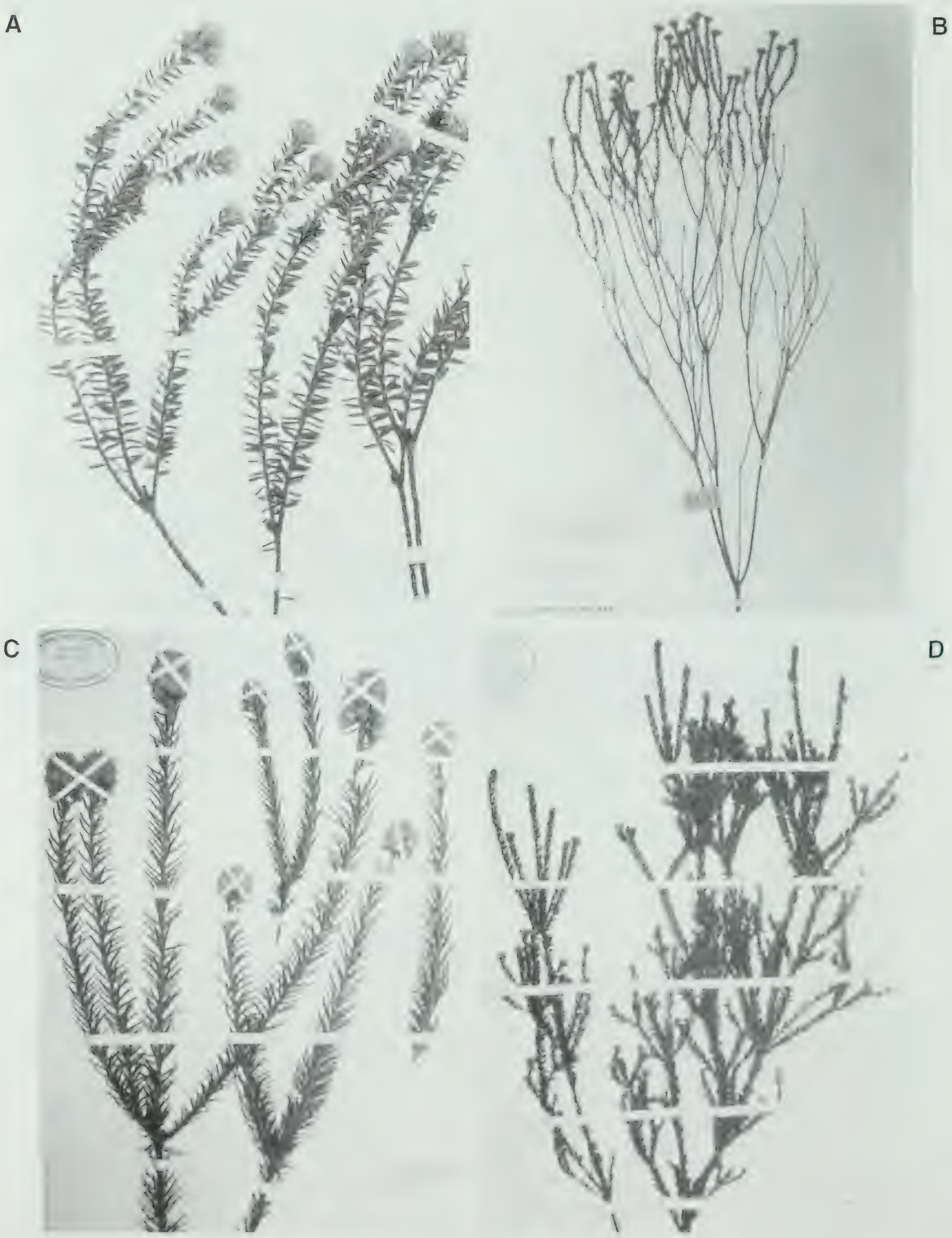


Figure 173 - **Staavia.** *A*, S. capitella *(Goldblatt 1813, NBG), B,* S. radiata *(Garside 4437, B), C,* S. zeyheri *(Williams 752, NBG), D,* S. verticillata *(Esterhuysen 35268, NBG).*

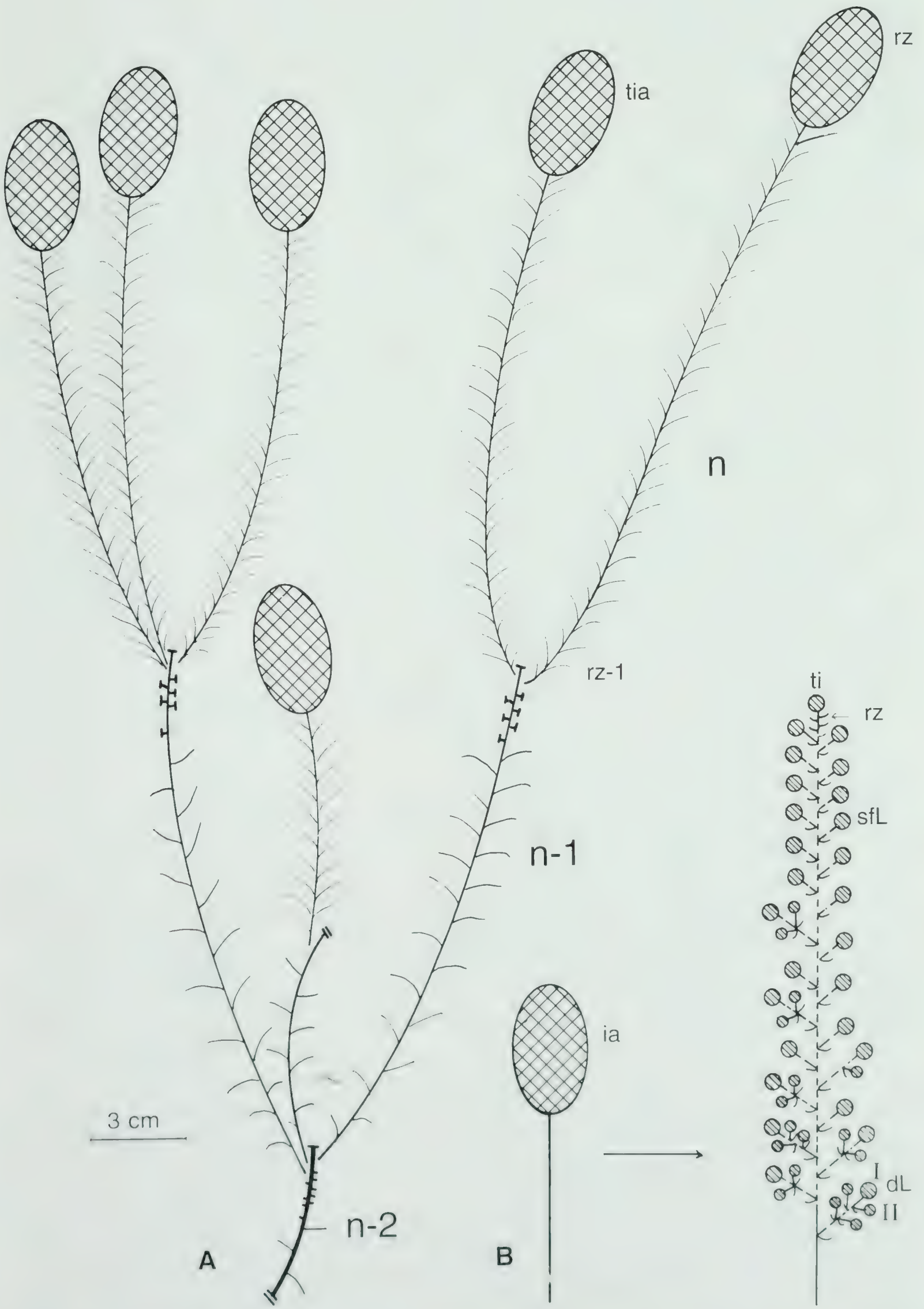


Figure 174 - **Staavia zeyheri**. *A, profile of a flowering shoot system, three seasons old, with terminal inflorescence aggregates. B, profile of a large inflorescence aggregate composed of a terminal inflorescence and numerous lateral flowering short-shoots, some of them with additional inflorescences of 2nd order of branches.* ia, *aggregate of inflorescences.*

florescence or also dies off without flowering. Each SGU has four to six sylleptic lateral shoots in a medial-distal position; these either flower terminally (sfL) and then show the characteristic sympodial branching pattern of the genus (fig. 175B) or remain vegetative (svL), emulating the mother axis in growing on during the next season (mc'). The lateral shoots are usually unbranched. Only occasionally do shoot systems with a high capacity for branching and renewal, similar to the dominant shoot, arise from lateral shoots (fig. 175A).

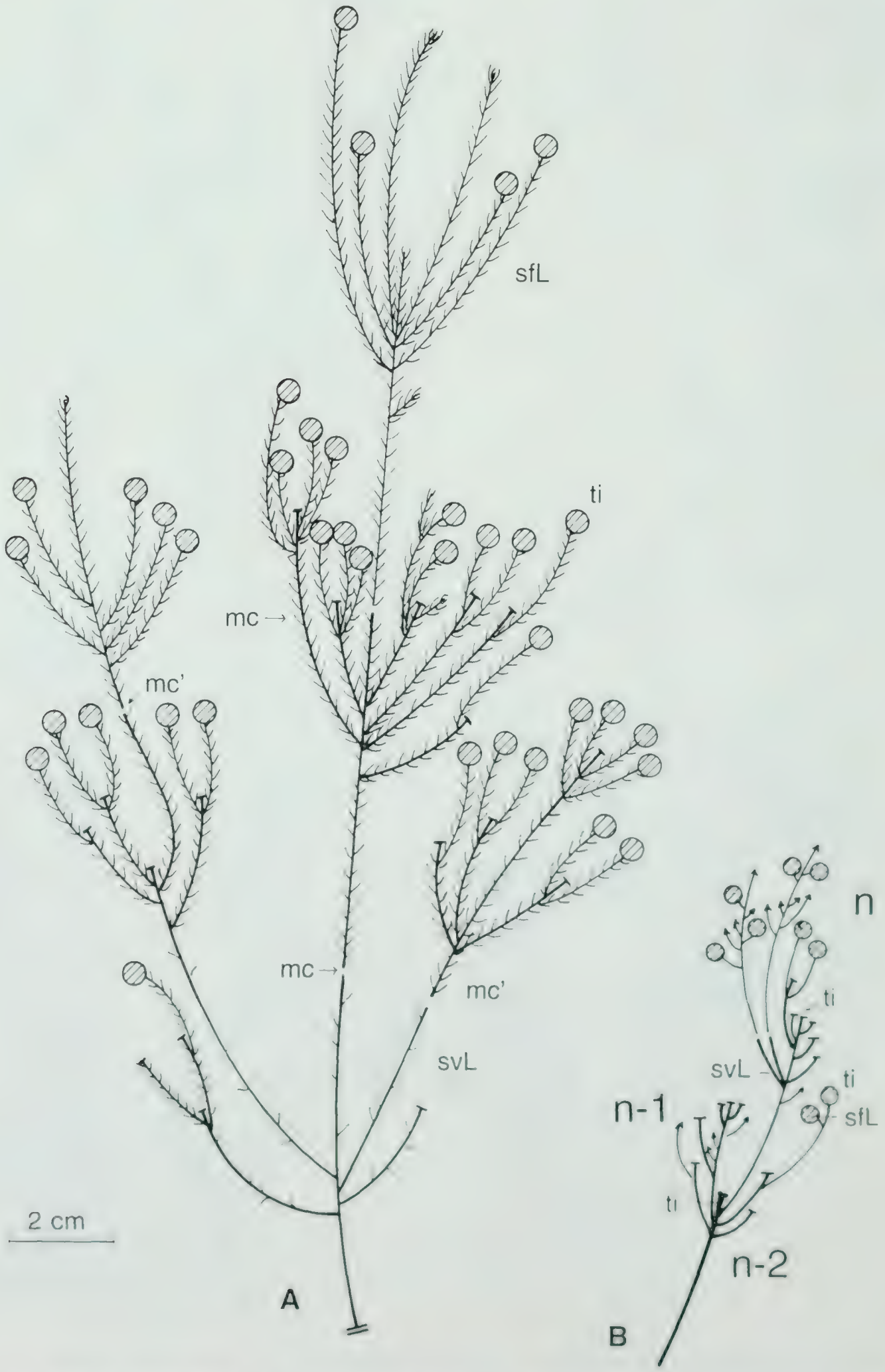


Figure 175 - **Staavia verticillata**. *A, profile of a flowering shoot system, two seasons old, B, profile of a lateral shoot system. Note the monopodial connection in A and the sympodial branching pattern in B*

Leaf metamorphosis and inflorescence structure. The apparent similarity between the capitate inflorescences of *S. glutinosa* (fig. 177) and *S. dodii* (fig. 176) and those of some Asteraceae suggests that the head-like inflorescences of the genus *Staavia* are also organized like simple open capitula. However, the first impression is deceptive in that the presence of a terminal flower could be demonstrated in each species studied.

Ontogenetic studies (fig. 176E) reveal that the individual inflorescence of *S. dodii* is crowned by a terminal floret which develops and opens first. The sequence of development is centrifugal (arrow). Each axillary floret is subtended by a bract and has at least two prophylls (pp) which gradually develop from the centre to the periphery. The centrifugal development is reflected in the flowering sequence which is likewise centrifugal and not centripetal as suggested by Moll & Gubb (1981). Before flowering the buds, flower-subtending bracts and prophylls are light-brown (fig. 176A). After anthesis they change colour and the whole centre becomes black (fig. 176B, 177C).

All *Staavia* species studied are characterized by cephaloids with a descending flowering sequence (fig. 178: arrows). Usually each floret has two prophylls. In *S. verticillata, S. capitella, S. dregeana, S. zeyheri* and *S. radiata* (fig. 178A-D′) five to ten florets come to flower while a further five to seven proximal primordia remain inhibited. Usually only one or two florets are open at the same time, demonstrating a clearly successional flowering sequence. As shown in fig. 178A-C the proximal florets are subtended by involucral bracts while the inner florets have much smaller subtending bracts. Only in *S. radiata* (fig. 178D, D′) are all subtending bracts petaloid. In *S. dregeana, S. verticillata* and *S. capitella* several sterile bracts surround the terminal floret (A,B), in *S. radiata* are two conspicuous bracts usually present (fig. 178D,D′) while in the remaining species sterile bracts may or may not appear. The inhibition of the proximal floret primordia suggest an increasing influence of the vegetative part of the shoot which is best expressed by the presence of the vegetative primordia of the cataleptic renewal shoots immediately below the inflorescence. *S. dodii* and *S. glutinosa* agree with the remaining species showing the same dominance of the terminal floret, the descending flowering sequence, the inhibited floret primordia and the primordia of the renewal shoots (fig. 178E,F). However, their inflorescences are much larger with up to thirty florets each.

The genus *Staavia* is characterized by a tendency to form flower-like inflorescences. The appearance of the individual inflorescences and the leaf metamorphosis of the species studied are illustrated in fig. 179. It is clear that the size of the blossom is positively correlated with the gradual transformation of the leaves from green assimilatory organs to white semaphylls. Concerning the appearance of the inflorescences two groups are distinguishable.

- The first group, represented by *S. verticillata, S. capitella, S. dregeana* and *S. zeyheri* (fig. 179A-D), is characterized by small relatively inconspicuous bowl-shaped inflorescences whose florets are embedded in long receptacular hairs. The involucral bracts scarcely differ from the uppermost green leaves. In *S. zeyheri* they increase slightly in length (fig. 179D′) and form a small involucre (D) as they do in *S. dregeana* (C), where the inner involucral bracts are a pale green and thus somewhat more conspicuous than the leaves below (fig. 169C).
- The second group is represented by *S. dodii* and *S. glutinosa* (fig. 179F, G). Both species have large and conspicuous inflorescences with strawy semaphylls and dark centres. The outermost involucral bracts clearly increase in length and lack chlorophyll except in a small area at the base (fig. 177A). Thus, they appear white. They persist for a long time. Though the involucral bracts are of different lengths they form a regular involucre round the receptacle, which bears the florets and their subtending bracts and prophylls. The receptacular hairs are not conspicuous. Prior to anthesis the sepals protect the florets. They are light-brown in colour with a reddish apex (fig. 176A, 177B) as are the remaining bracts. The overall impression of the central portion of the inflorescence is one of uniformity. During anthesis the florets open successively and their individual character is apparent (fig. 176B, 177C). After anthesis the florets lose their individuality and become part of the black amorphous centre. During fruiting three to five light-brown capsules arise from the black centre and release their seeds (fig. 176C).

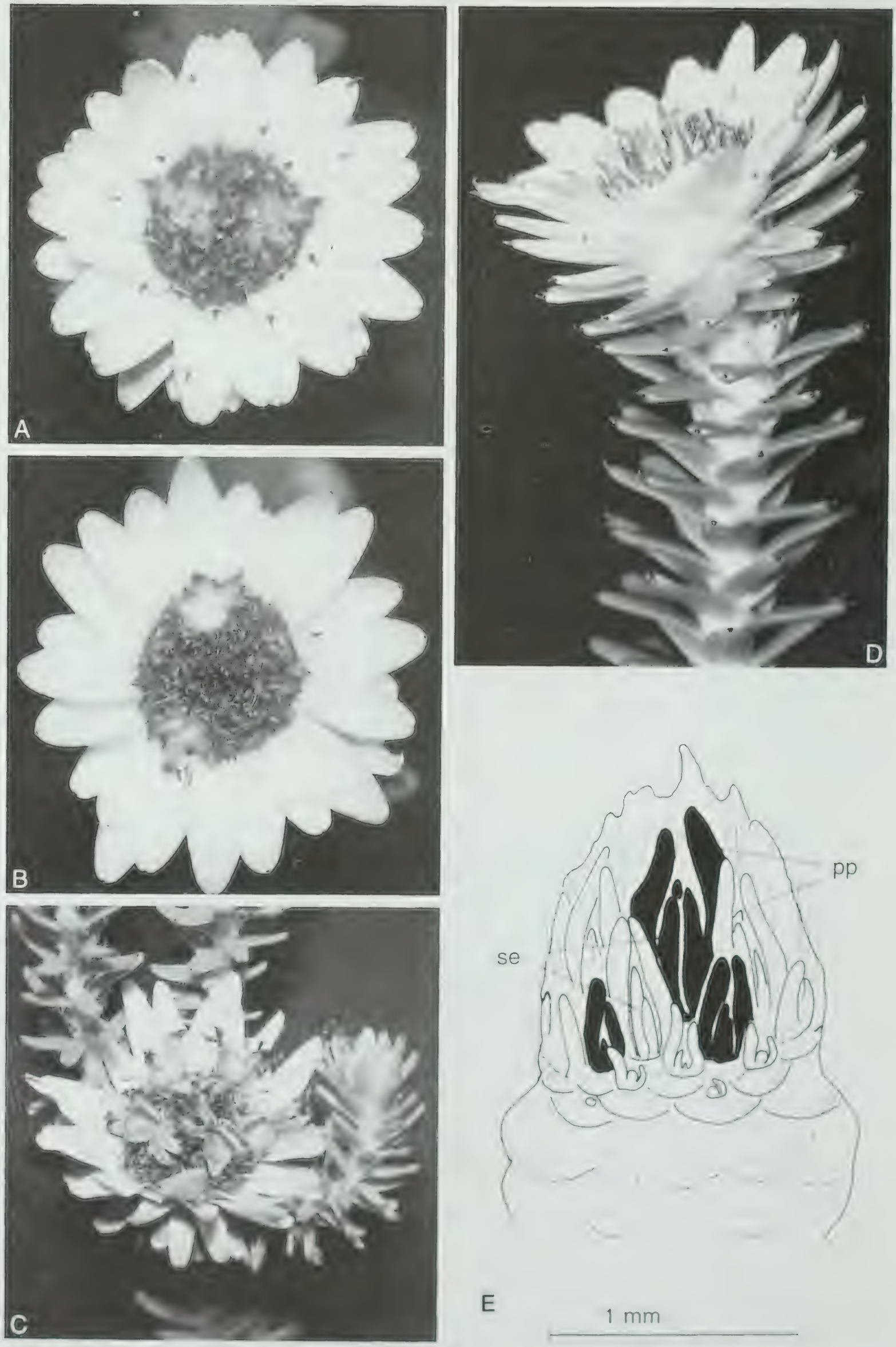


Figure 176 - **Staavia dodii**. *A-C, flower-like inflorescences of different age showing the centrifugal flowering sequence of the individual florets (after flowering the colour changes to black), D, lateral view of an inflorescence showing the more or less abrupt leaf metamorphosis from green to white leaves, E, ontogenetic stage of the inflorescence showing the centrifugal development of the floret primordia*

pp, *prophyll*, se, *sepal*

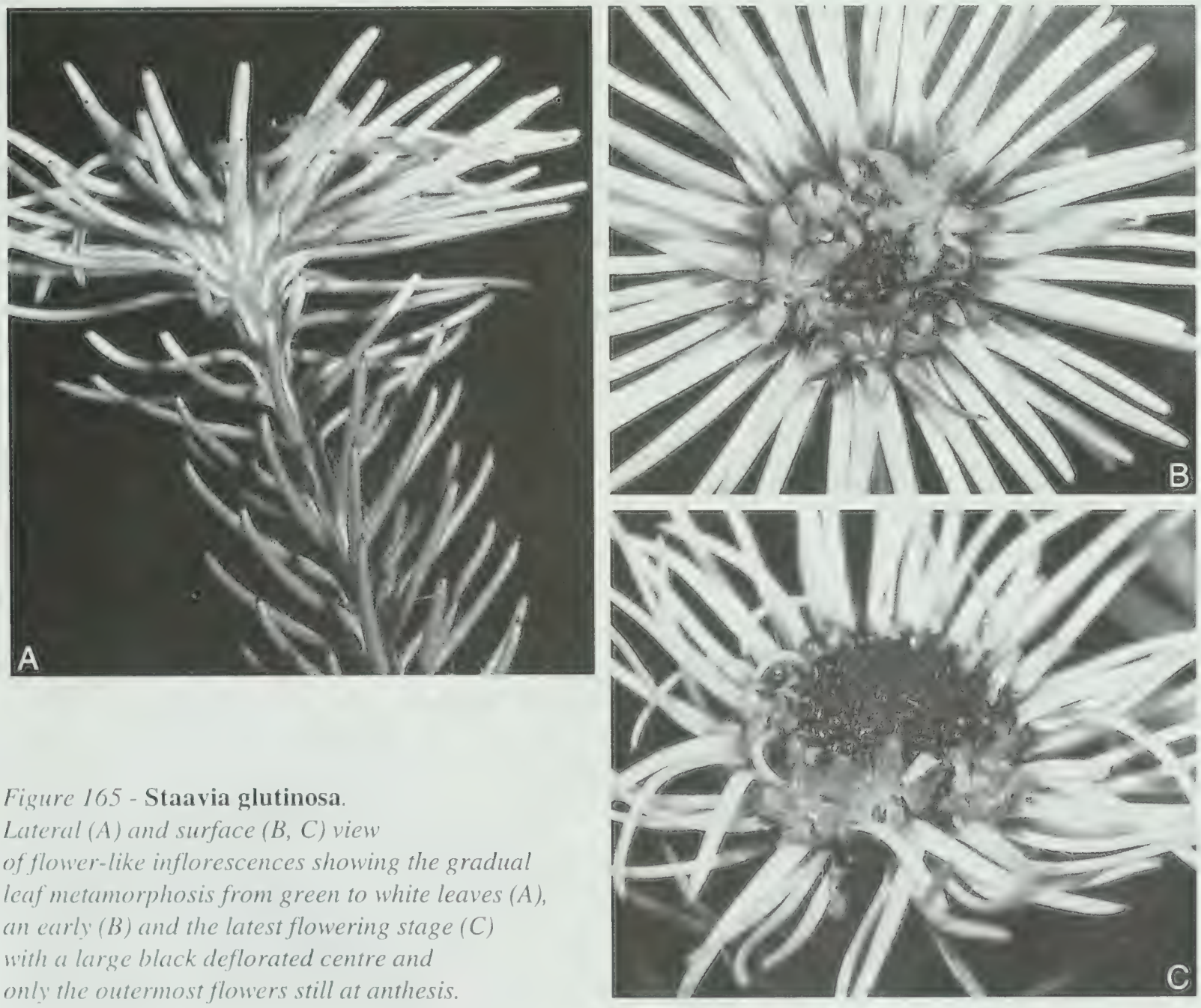


Figure 165 - **Staavia glutinosa**.
Lateral (A) and surface (B, C) view of flower-like inflorescences showing the gradual leaf metamorphosis from green to white leaves (A), an early (B) and the latest flowering stage (C) with a large black deflorated centre and only the outermost flowers still at anthesis.

The inflorescence of *S. radiata* (fig. 168B, 179E,E′) appears intermediate between the two groups. It shares the small size and bowl-like form with the first group and the conspicuous strawy involucral bracts surrounding a dark centre, with the second group. The involucral bracts are white only in the upper half, remaining greenish below. Some of the central bracts appear similar and the clear boundary between centre and periphery of the inflorescence is less defined (fig. 178D′).

Summary. Branching pattern and flowering behaviour in the genus *Staavia* is illustrated in fig. 180. The reference system (A) shows the terminal inflorescence (a cephaloid), the subfloral renewal zone and the branching zone with sylleptic flowering lateral shoots.

With the exception of *S. verticillata* all species of the genus show a regular sympodial branching pattern, forming one sympodial unit in one season. However, as regards SGU lengths and number of lateral shoots, a high degree of variability was found (C) It was frequently noted that only the terminal inflorescence or a triad comprising a terminal and two closely aggregated lateral inflorescences were present. In *S. glutinosa* flowering shoots also appear in the medial zone of the SGU (C: me). In *S. zeyheri* compound inflorescences are formed (*A*) comprising the terminal and up to 45 lateral inflorescences of 1st and 2nd order of branches. However the renewal zone remains below the terminal inflorescences and thus the compound inflorescence differs from that found in two *Nebelia* species

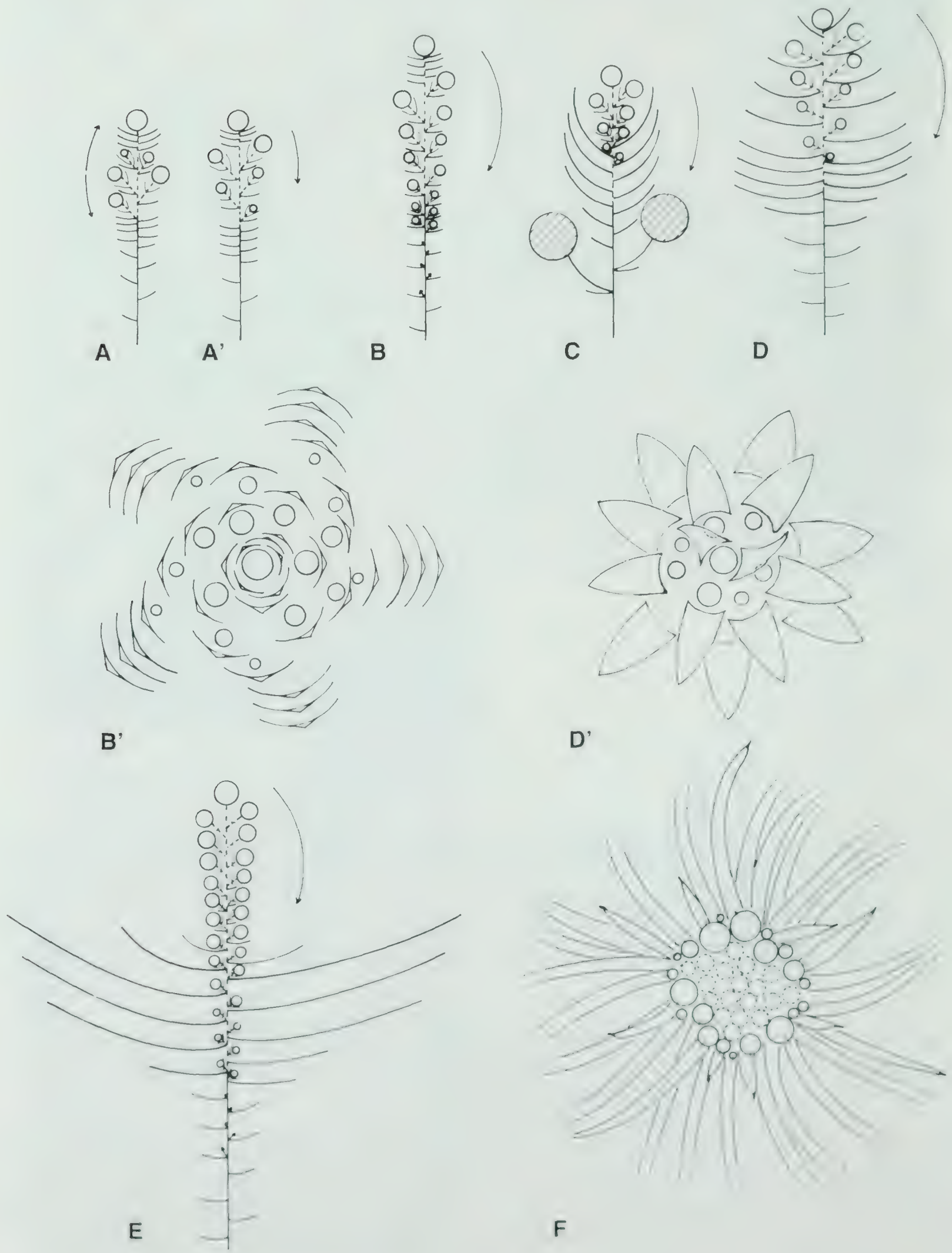


Figure 178 - **Staavia**. ***Inflorescence structure***. *Profiles and diagrams of the inflorescences of A,A'*, S. verticillata, *B,B'*, S. capitella, *C*, S. zeyheri, *D,D'*, S. radiata, *E*, S. dodii, *F*, S. glutinosa.
The arrows illustrate the flowering sequence

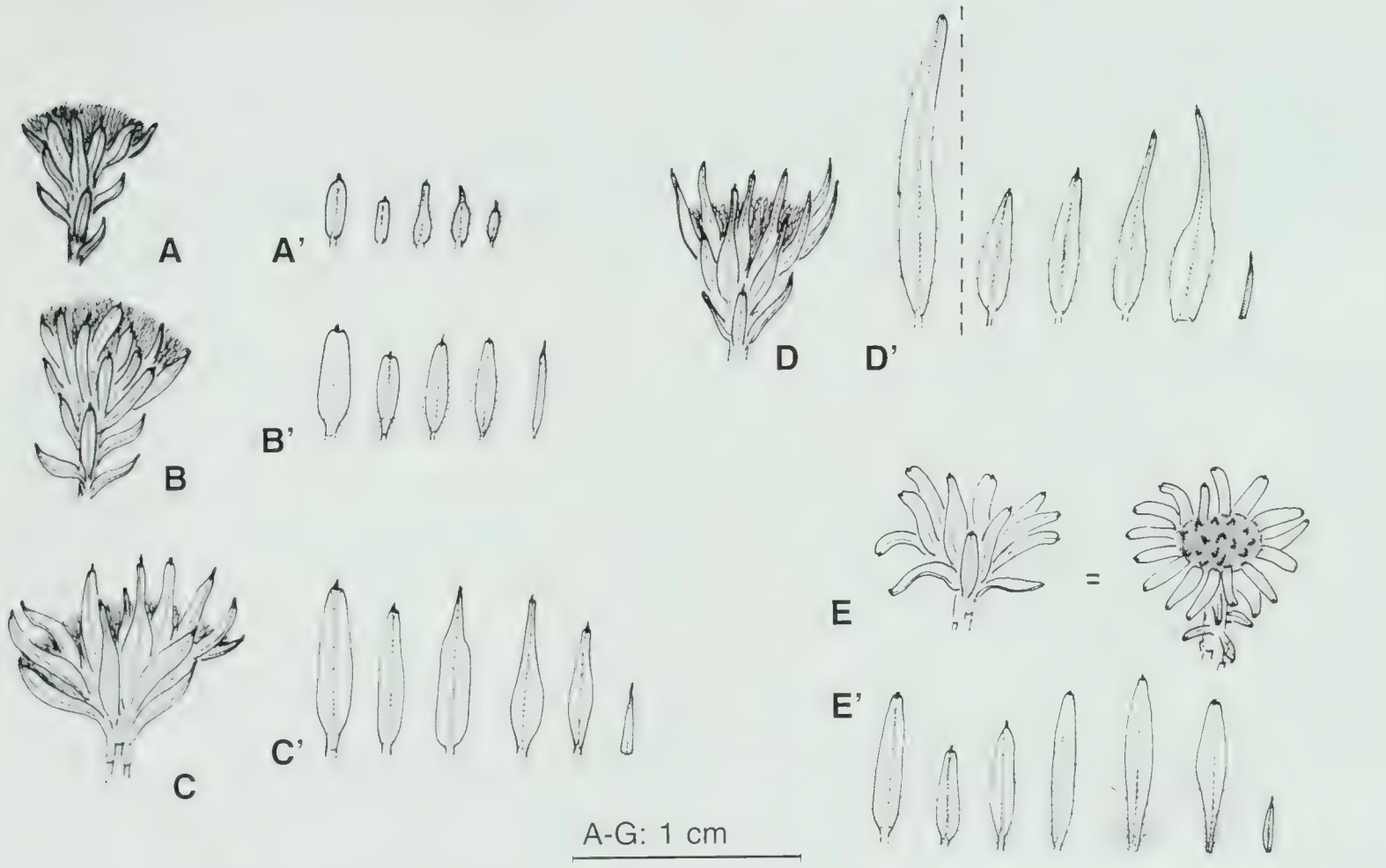


Figure 179 - **Staavia**. ***Formation of flower-like inflorescences***. *A-G, appearance of the inflorescence, A'-G', leaf metamorphosis, from left to right: green leaves, outer and inner involucral leaves (= outer flower-subtending bracts), inner flower-subtending bracts. A,A'*, S. verticillata, *B,B'*, S. capitella, *C,C'*, S. dregeana, *D,D'*, S. zeyheri (the dotted line points to the different order of branches of the green leaf and the involucral leaves), *E,E'*, S. radiata, *F,F'*, S. dodii, *G,G'*, S. glutinosa.

In most cases all shoots terminate in an inflorescence. However, weak renewal shoots may remain vegetative for the first season and come to flower only in the following season (D: cvR). They do not influence the habit of the shoot system concerned.

In contrast to the remaining species, in *S. verticillata* the apex of the main axis remains vegetative and continues to grow for at least two seasons (B: mc). The result is a dimorphism between a long dominant shoot several seasons old and shorter regularly sympodially branched lateral shoot systems.

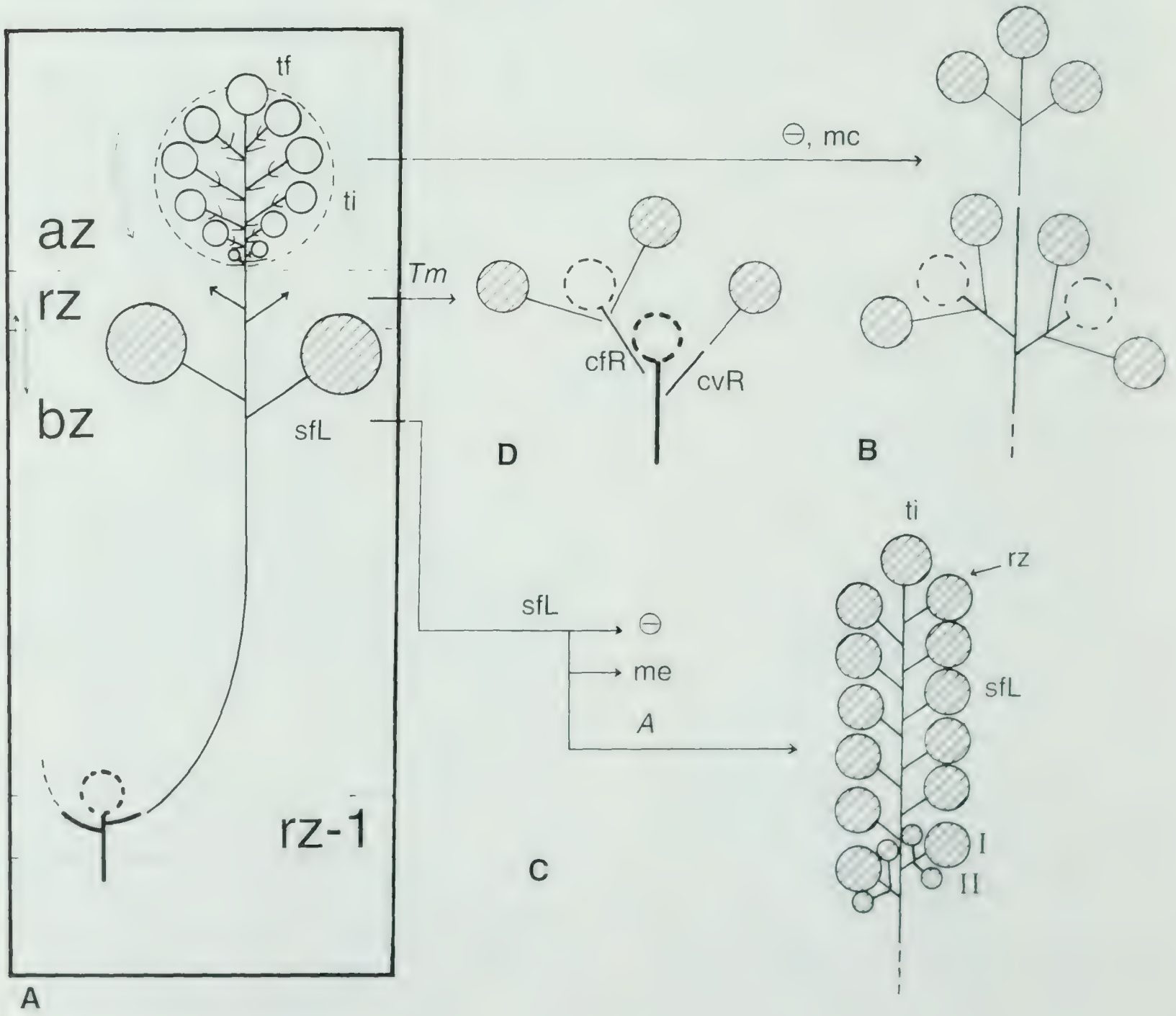


Figure 180 - ***Model of the genus* Staavia**. *A, reference system with terminal cephaloid, subfloral renewal zone and branching zone with a few distally arranged sylleptic flowering lateral shoots. B-D, variations in behaviour (B) of the apex which occasionally remains open and continues to grow on in* S. verticillata (mc), *(C) of the sylleptic flowering lateral shoots which are occasionally absent, arranged in the medial part of the branching zone (*mc; S. glutinosa*) or as in* S. zeyheri *form an inflorescence aggregate with the terminal inflorescence and (D) of the flowering chronology (Tm).*

cvR, *cataleptic vegetative renewal shoot,* Tm, *shifting in time.*

3.11 *Thamnea* Soland. ex Brongn.

Thamnea *is characterized by solitary terminal flowers which are surrounded by numerous involucral bracts. The genus has seven species, two of which are presumed extinct (Hilton-Taylor 1996).* T. massoniana *was studied at the summit of Victoria Peak (fig. 181). Only a few herbarium specimens of* T. diosmoides, T. hirtella, T. gracilis *and* T. thesioides *were available for the present study. Thus, the analysis remains fragmentary.*

Growth and branching pattern. According to Pillans (1947:144) all species are low (10-50 cm in height), densely branched shrubs of rocky montane habitats (2000-6000 ft).

T. massoniana (fig. 183A) is a rock-crevice species characterized by a predominantly prostrate habit. As fig. 183 A′,A″ illustrates, the branching pattern is exemplary for epitony and hypotony. Each SGU terminates in a flower (tf) and is renewed by lateral shoots below the terminal flower (rz). The hypotonic renewal shoot (R_{hy}) is most dominant, prolonging the plagiotropic shoot system. It is unbranched except for a few sylleptic flowering lateral shoots (sfL). The remaining renewal shoots are always erect, sylleptically branched and able to form a sympodial shoot system several seasons old. The epitonic shoots (R_{ep}) are only slightly shorter than the hypotonic shoots and are characterized by a high branching capacity, while the amphitonic shoots (R_{am}) usually remain shorter and less branched. In contrast to fig. 183A, fig. 183B illustrates a symmetric flowering shoot system with renewal shoots nearly equal in length. It is suggested that this example is part of a lateral erect flowering shoot system which is not under positional influence.

The degree of branching and the number of flowers per SGU depend directly on the orientation of the renewal shoots in space. Branching pattern clearly influences plant habit. A shoot dimorphism results from the formation of both a dominant plagiotropic and numerous erect flowering shoot systems. The individual SGUs are similar in comprising a terminal flower, a subfloral renewal zone and a zone with sylleptic flowering lateral shoots. But, depending on the specific development of the renewal shoots, they either acquire an asymmetric prostrate (fig. 183A) or a symmetric habit (fig. 183B).

In *T. diosmoides* (fig. 184A, 185) the shoot system also comprises prostrate leaders and erect flowering shoots. Here, too, the orientation in space influences the length and branching capacity of the renewal shoots. As in *T. massoniana*, each shoot terminates in a flower, but in *T. diosmoides* monopodial units (mc) may arise before the terminal flower is able to force sympodial branching once more.

Figure 181 - **Thamnea massoniana**. *Locality at the summit of Victoria Peak (6200 ft), Hottentots Holland Nature Reserve. In the foreground a fynbos community with Restionaceae and Ericaceae (about 4300 ft) is shown.*

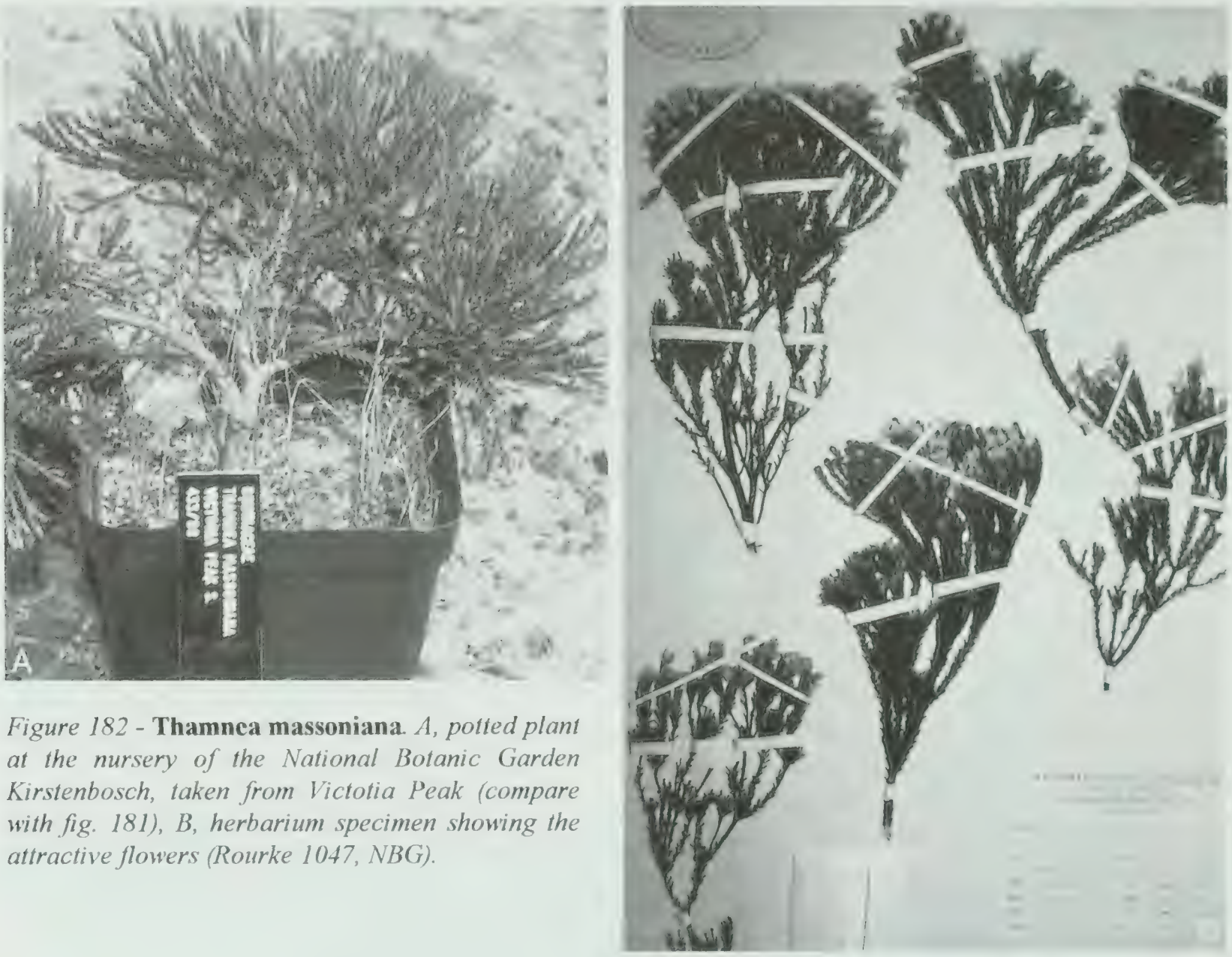
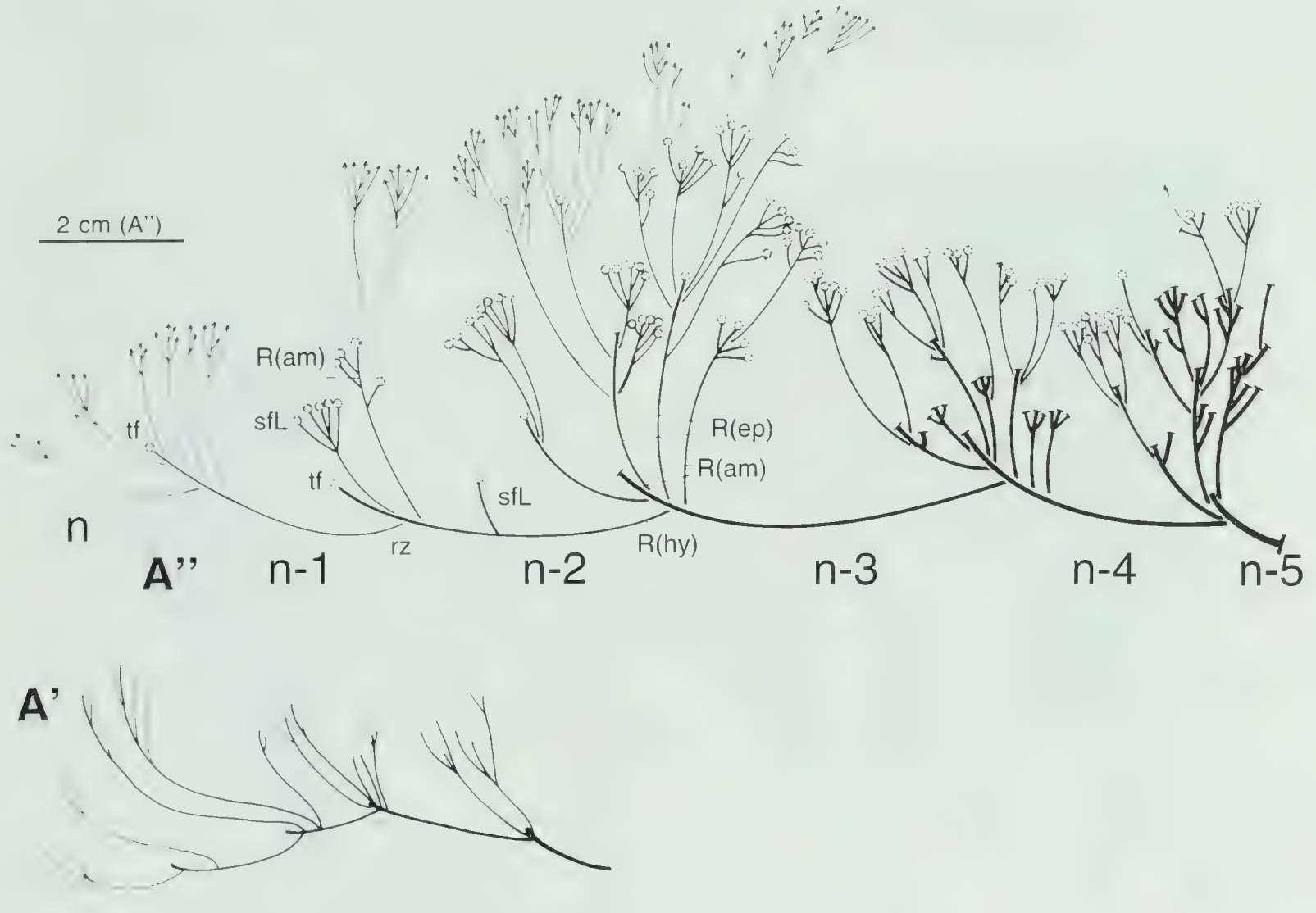


Figure 182 - **Thamnea massoniana**. *A, potted plant at the nursery of the National Botanic Garden Kirstenbosch, taken from Victotia Peak (compare with fig. 181), B, herbarium specimen showing the attractive flowers (Rourke 1047, NBG).*

The individual SGU bears many sylleptic flowering lateral shoots (sfL), mainly in the proximal and medial zone and cataleptic flowering lateral shoots (cfL) in the distal zone. Occasionally sylleptic vegetative lateral shoots (svL) also appear (fig. 185 C). In case of a monopodial SGU connection (mc) the proximal lateral shoots are dominant thus repeating the main axis as regards branching pattern (fig 185A). Presumably the primordia of prospective renewal shoots are formed irrespective of the presence or absence of a terminal flower. These either become the dominant proximal sheots of the next SGU, or its cataleptic renewal shoots.

The remarkable growth form of the shoot system in *T. hirtella* (fig. 184B) is caused by lateral shoots which overarch the mother axis (fig. 186B, B´). This gives rise to a creeping habit. However, in contrast to *T. massoniana*, the epitonic rather than hypotonic shoots are most dominant.

The dominant shoot in fig. 186B, B´ comprises several monopodial units (mc). It is not clear whether the apex finally forms a terminal flower or dies off without flowering, but it is apparent that sympodial branching starts from subterminal renewal shoots (rz). The individual SGU has numerous sylleptic flowering lateral shoots (sfL) which are usually short and unbranched, but able to continue growth in a sympodial manner. Individual lateral shoots in the medial region (me) of the SGU may remain indeterminate (n-2 iL), these have sylleptic flowering lateral shoots of 2nd order of branches (II) and continue growth in a monopodial manner (mc´) as does the dominant shoot. They may renew the whole shoot system two seasons later (n) when the apex of the formerly dominant shoot has died off. A cataleptic flowering shoot system (cL) may in addition arise from the medial part of the SGU concerned (n-2) and is capable of renewing the shoot system. The shoot system illustrated in fig. 186B, B´ shows the existence of two different renewal systems: (1) the probable original renewal zone below the apex/terminal flower, which appears to have become more or less ineffective as evidenced by the



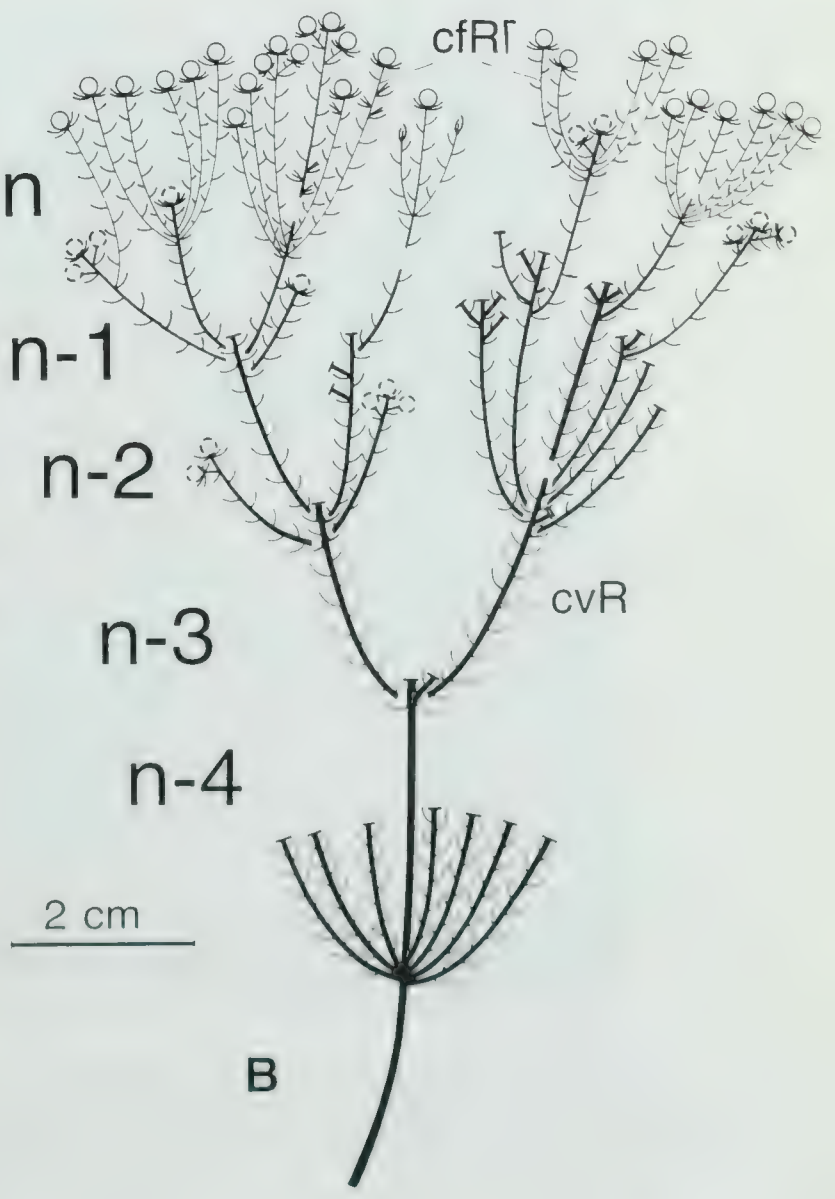


Figure 183 - **Thamnea massoniana**. *A, appearance (Claßen & Esterhuysen 1418, CLA), A', branching pattern and A'' profile of a flowering shoot system, six seasons old, B, profile of a flowering shoot system, five seasons old. Note the differences between the hypotonic and epitonic shoots in the prostrate shoot system (A-A'') and the equal length of the lateral shoots in the orthotropic shoot system (B).*

am, *amphitonic*, cvR, *cataleptic vegetative renewal shoot*, ep, *epitonic*, hy, *hypotonic*.

prostrate growth form, the monopodial shoot connection and the lack of hypotony and (2) the mesotonic-epitonic shoots which are present independent of the mode of shoot connection and which are able to overtop the creeping shoot system and thus gain space and light.

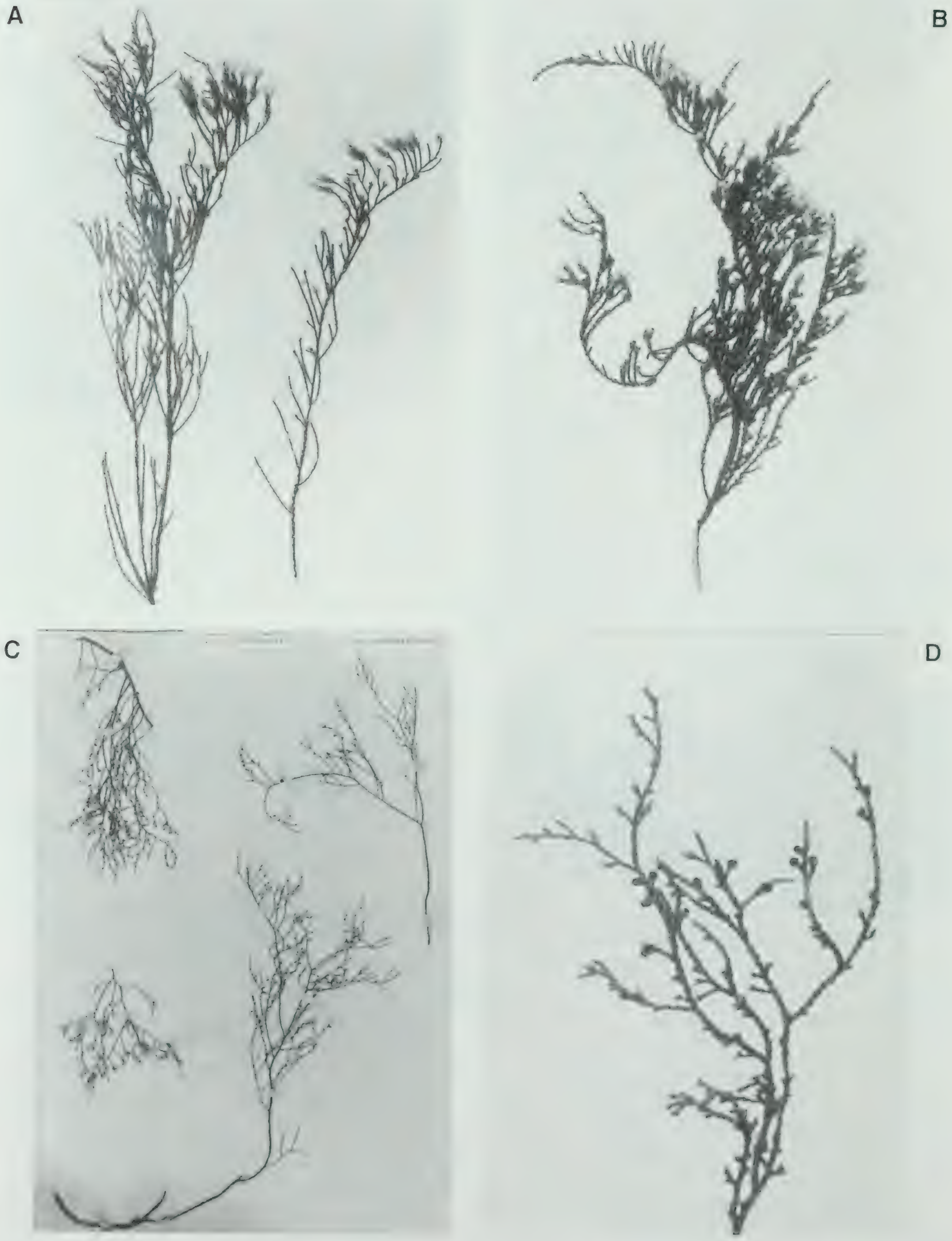
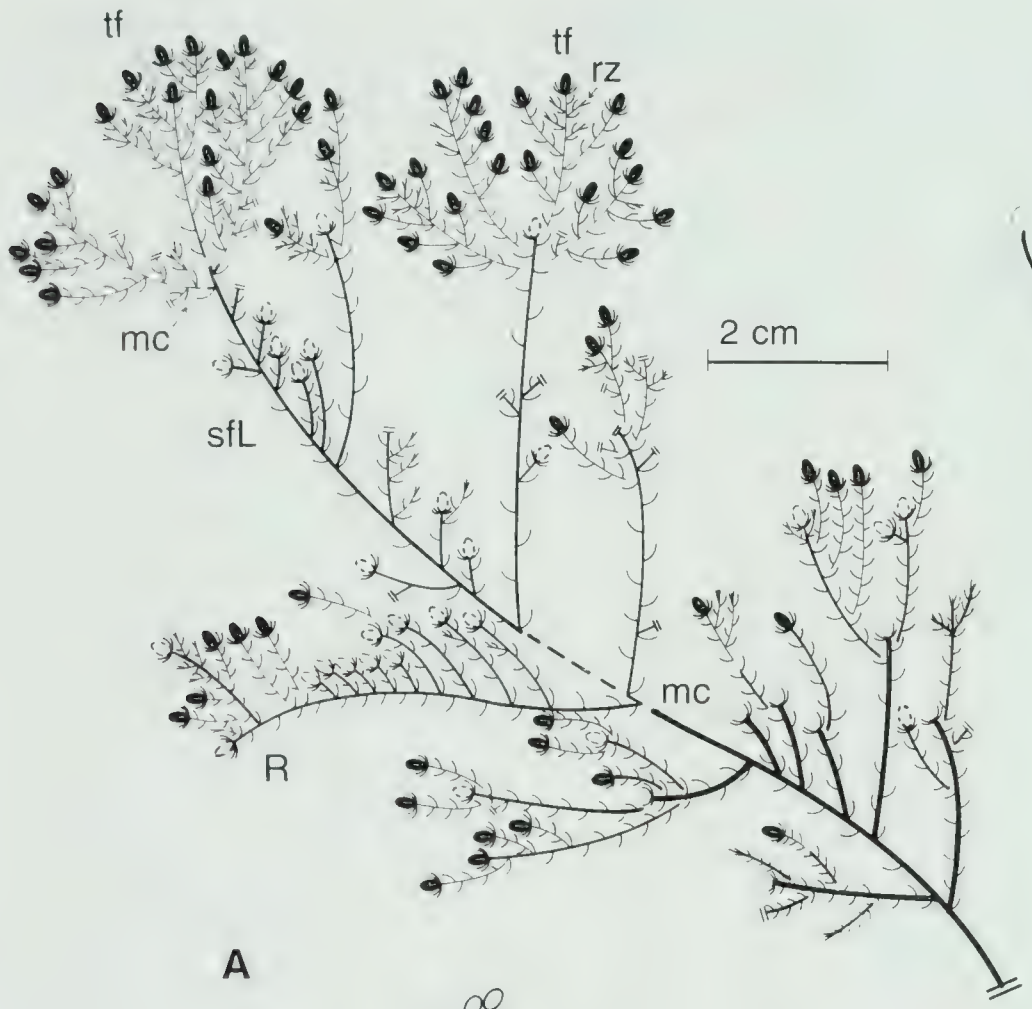
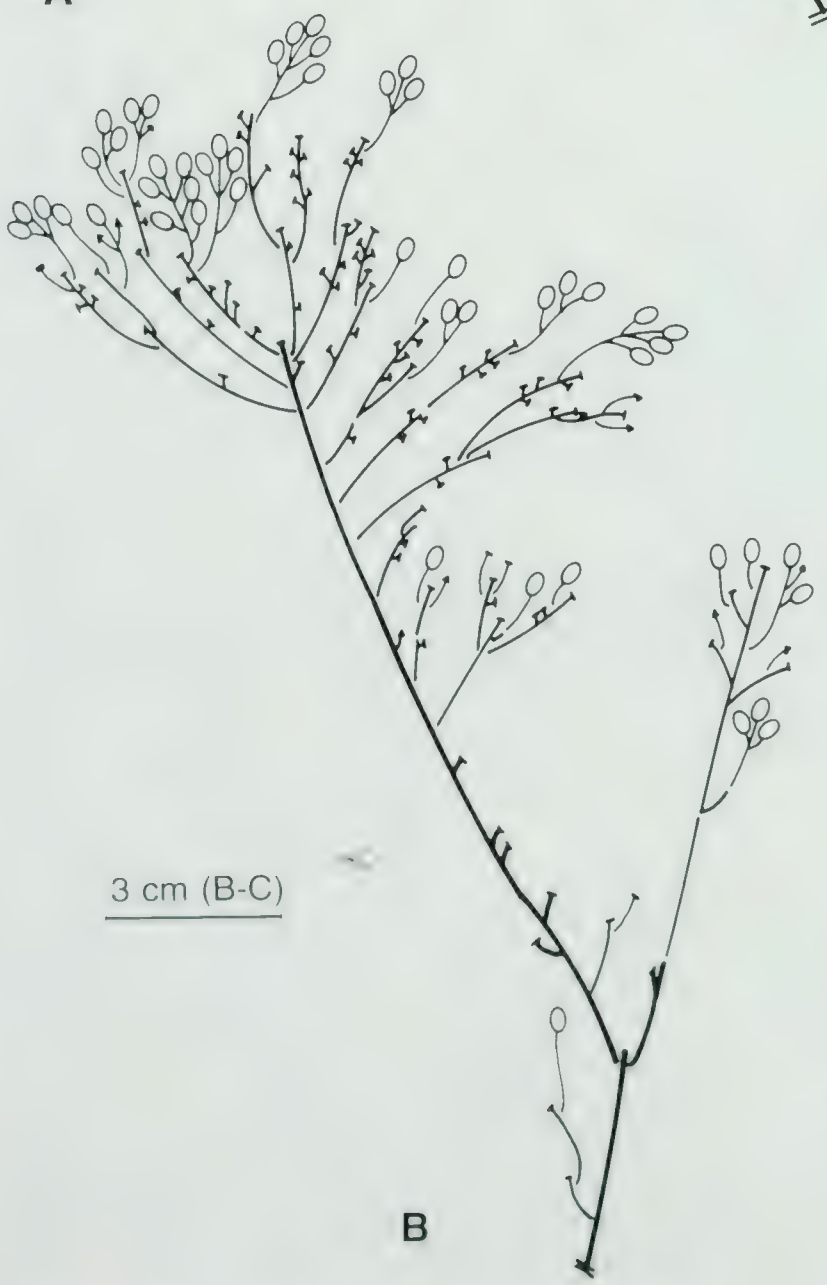


Figure 184 - **Thamnea**. *A*, T. diosmoides (Carlquist 4665, B), *B*, T. hirtella (Esterhuysen 25765, B), *C, D*, T thesioides. *(Schlechter 419, B; Esterhuysen 35408, NBG)).*

Compare A with fig. 185, B with fig. 186 and C,D with fig. 188





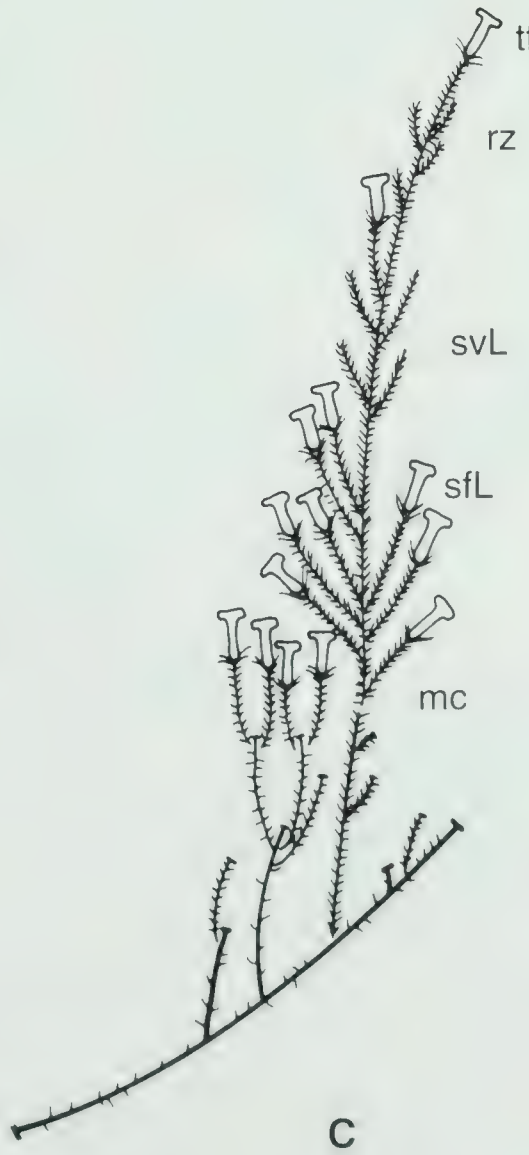


Figure 185 - **Thamnea diosmoides**. *A, profile and A', branching pattern of a flowering shoot system, B, C, profiles of flowering shoot systems, illustrating (C) the solitary position of the attractive flowers.*

Compare with fig. 184A

Fig. 186A, A´ illustrates a second shoot system which appears to be oriented in a more orthotropic manner. The dominant shoot of unknown age terminates in a flower. Several lateral flowering shoot systems show a regular sympodial branching pattern. Presumably in *T. hirtella* the degree of sympodial branching and the behaviour of the apex depend on the orientation of the shoot system in space, as in the case of *T. massoniana*.

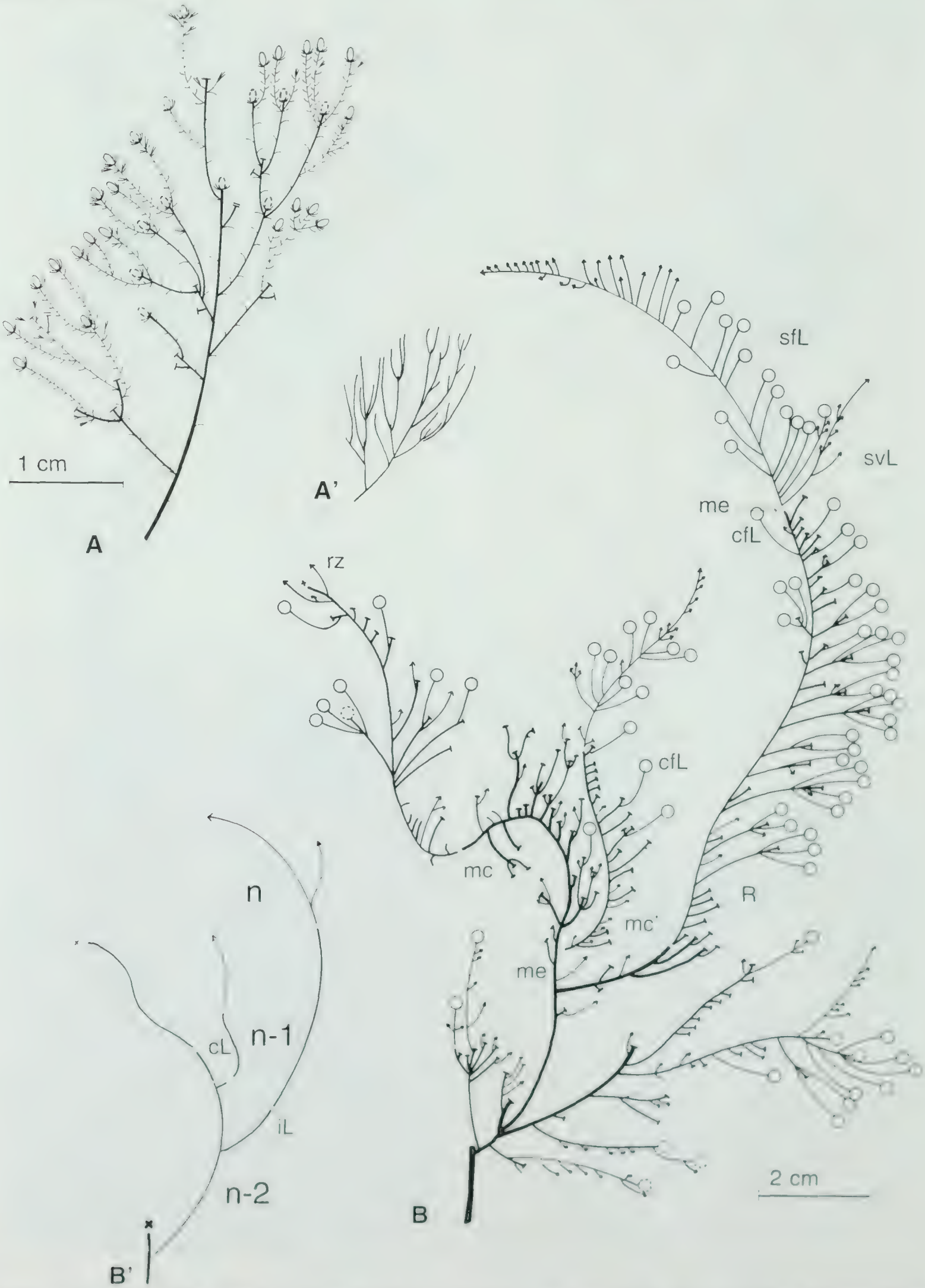


Figure 186 - **Thamnea hirtella**. *A, profile and A´, appearance of a flowering shoot system, B, profile and B´, branching pattern of a flowering shoot system, three seasons old*

cL, *cataleptic lateral shoot; compare with 184B*

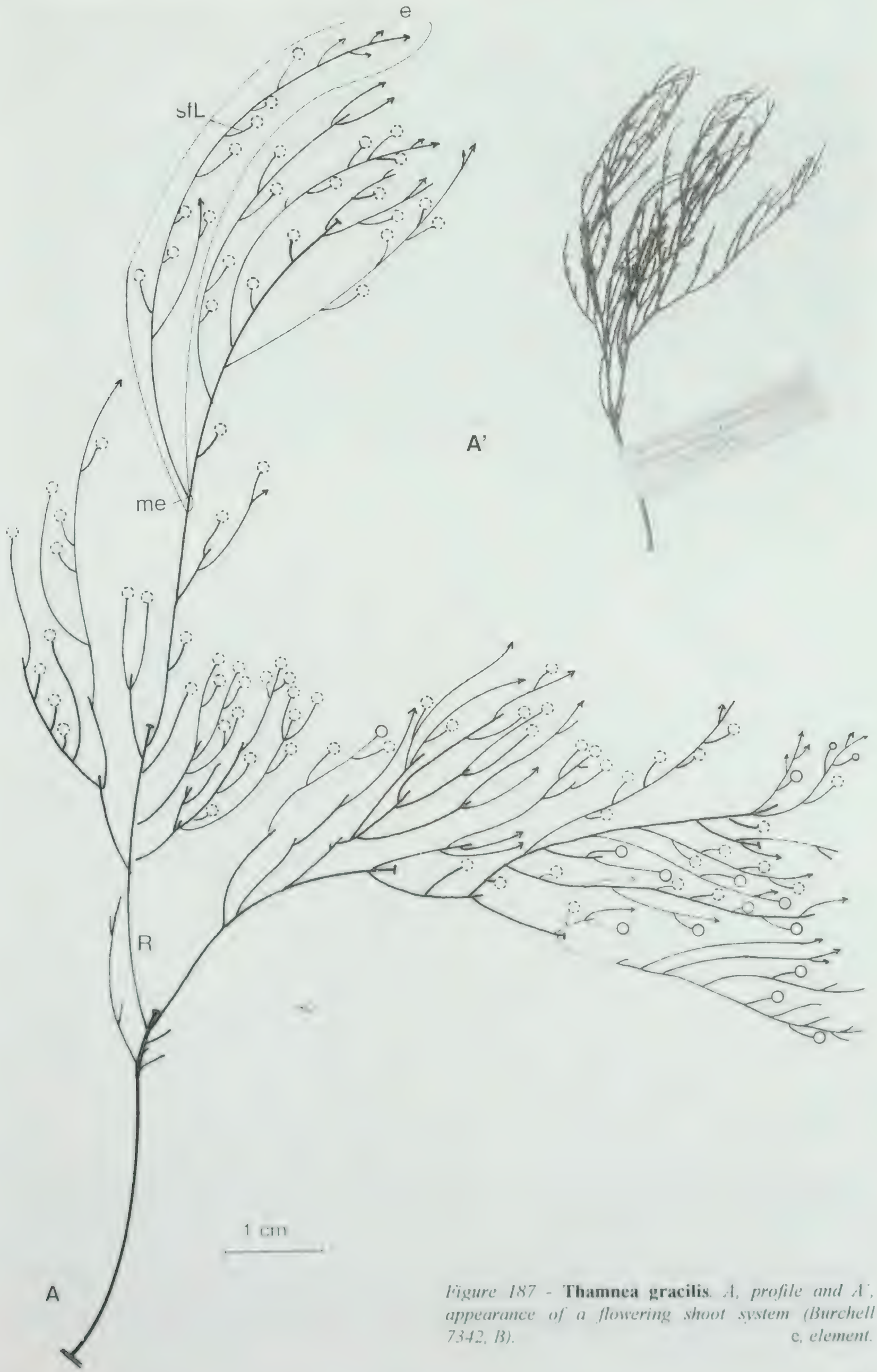


Figure 187 - **Thamnea gracilis**. *A, profile and A', appearance of a flowering shoot system (Burchell 7342, B).* e, *element.*

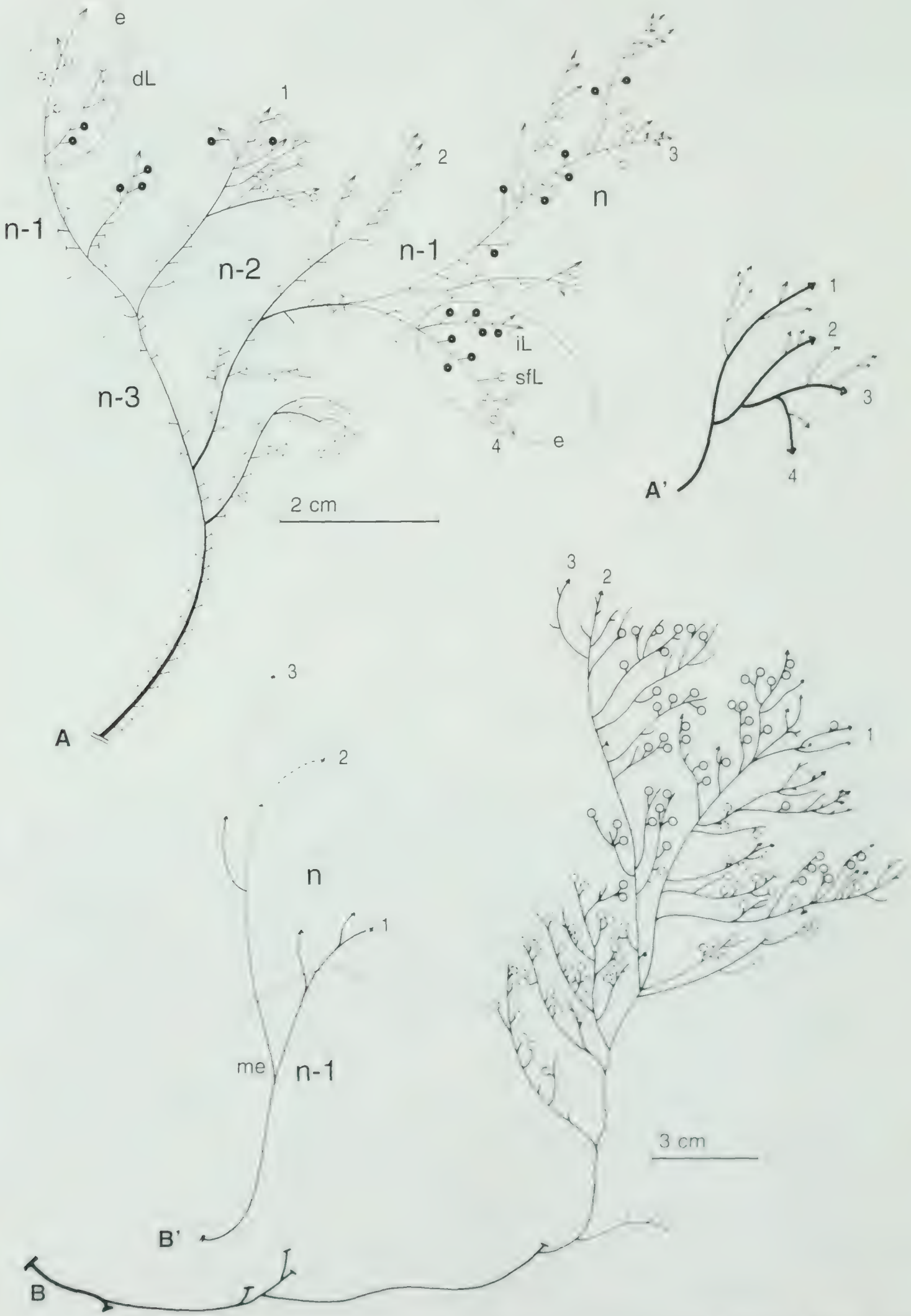


Figure 188 - **Thamnea thesioides**. *A, B, profiles and A', B', branching patterns of flowering shoot systems, in A presumably five seasons old.* e, *element; compare with fig. 184 C, D.*

T. gracilis (fig. 187A') and *T. thesioides* (fig. 184C,D) differ from the remaining species studied in the reduced nature of their shoot systems and their much smaller, inconspicuous flowers. It proved difficult to identify individual SGUs in both species and occasionally impossible to decide whether a shoot had arisen laterally or terminally.

- The shoot system of *T. gracilis* (fig. 187A) is characterized by slender, slightly curved leader shoots (e) connected in a sympodial manner. The individual sympodial unit bears sylleptic flowering lateral shoots which are relatively short and unbranched and which continue growth in a sympodial manner for several seasons. The shoot system is usually renewed subterminally. Occasionally mesotonic shoots (me) which overtop their mother axis may arise and extend the shoot system during a succeeding season, as has been shown in *T. hirtella*. Probably each of the sympodial units corresponds to a SGU. However, when comparing the branching pattern with that of *T. diosmoides* the possibility exists that the supposed mesotonic shoot is in fact a prospective renewal shoot, which in case of a monopodial SGU connection appears as a lateral shoot. In this case, the shoot system illustrated would be five seasons old.
- *T. thesioides* (fig. 188) is clearly characterized by overtopping lateral shoots. However, it is very difficult to identify the individual SGUs. Formally the structure of the shoot system can be described by a specific element which is repeated again and again (fig. 188A: e); it is possible that this element corresponds to a SGU. It is composed of an indeterminate main axis which is able to grow on, thus connecting the elements in a monopodial manner. Some sylleptic flowering lateral shoots are present in the distal and medial zones and a much longer shoot in the proximal region. The proximal shoot either forms a terminal flower (dL) or more often remains indeterminate (iL) and repeats the branching pattern of the mother axis. In this manner it is able to overtop the mother axis and to renew the whole shoot system.

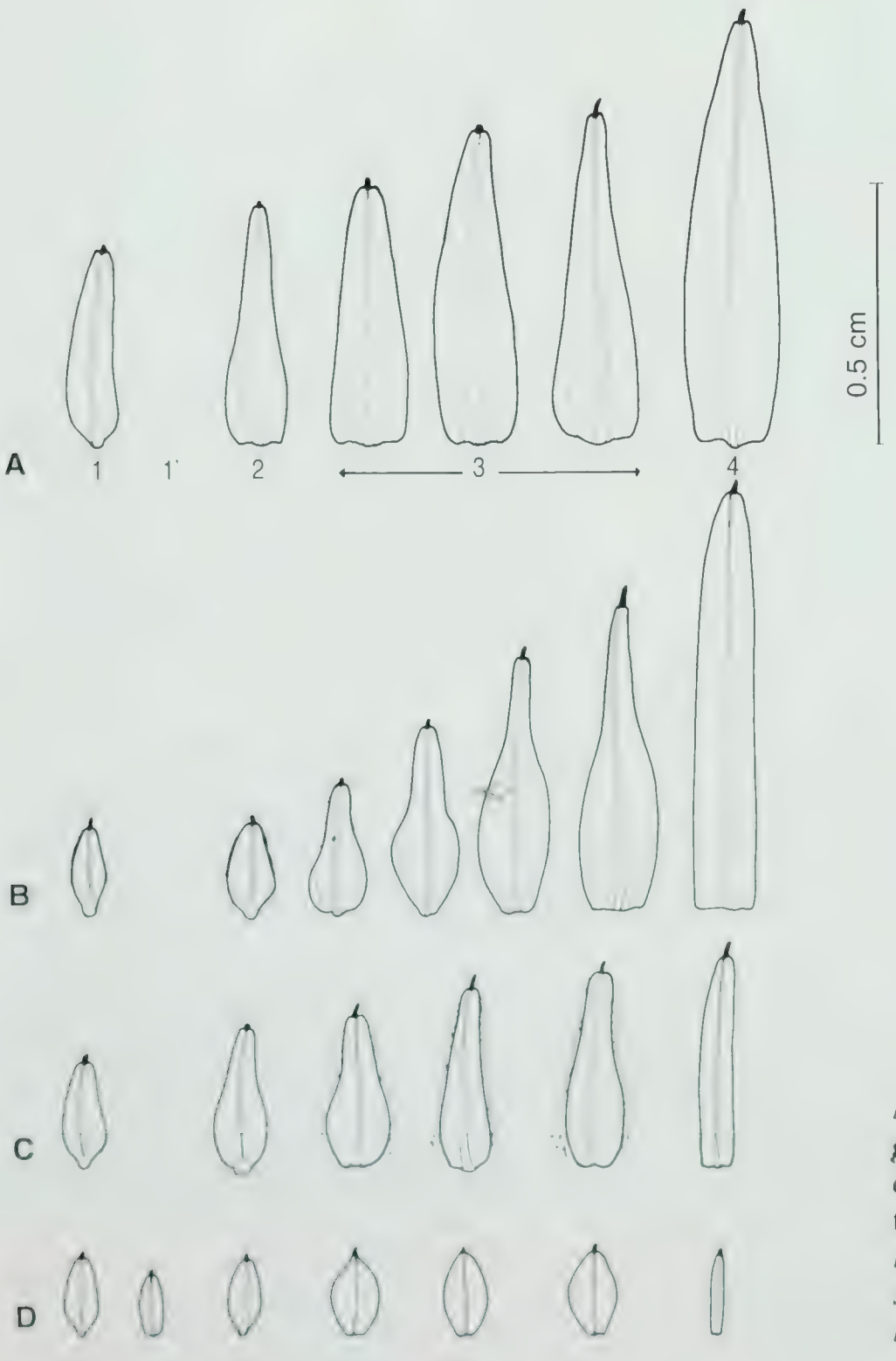


*Figure 189 - **Leaf metamorphosis in the genus* Thamnea. *A*, T. massoniana, *B*, T. diosmoides, *C*, T. hirtella. *D*, T. thesioides. *1: leaf at the main shoot, 1': leaf at the base of a lateral flowering shoot, 2: leaf below the involucre, 3: involucral leaves, 4: sepal.*

Leaf metamorphosis and inflorescence structure. The genus is characterized by solitary flowers which are arranged terminally on the main axis of the SGU and/or at the end of lateral shoots. Dependent on the flower arrangement, the appearance of the shoot systems differs. In *T. massoniana* the terminal flower (always present) forces a regular sympodial branching, while in *T. thesioides* the absence of a terminal flower results in a monopodial shoot connection and in a shoot dimorphism between the dominant leaders and the lateral flowering short-shoots. Nevertheless the latter are not lateral but, like the terminal flowers on the main axis, solitary flowers borne at the end of very short lateral shoots. The argument for a terminal (rather than lateral) position of the flowers borne on the lateral short-shoots is based very largely on leaf metamorphosis patterns, which are very similar in the main axis and lateral short-shoots.

Fig. 189 illustrates the leaf metamorphosis of four *Thamnea* species. Leaves are always present below the flower and some transitional leaves (2) occur between the small foliage leaves (1) and - *except T. thesioides* - the much larger involucral elements (3). Despite the gradual leaf metamorphosis, the involucre of ten to fifteen leaves is clearly differentiated from the foliage. The involucral leaves are always spread in contrast to the densely appressed foliage of *T. gracilis, T. diosmoides* and *T. thesioides*. They are either larger than the green leaves (A-C) or coloured (reddish) (*T. massoniana*), ciliate (*T. hirtella*) or notably thin and membranous (*T. thesioides*). As regards length, the involucral elements interpose between the leaves and the sepals of the terminal flower and may be 1,5x (*T. hirtella*), 2x (*T. massoniana*) or nearly 4x (*T. diosmoides*) longer than the leaves. The flowers of the cited species are large (0,7-1,5 cm) and attractive and in this respect very different to the small (2 mm long) flowers of *T. gracilis* and *T. thesioides*.

Summary. The genus is subdivided into two groups. The first, represented by *T. massoniana* and *T. diosmoides*, is characterized by large and attractive solitary flowers borne at the end of the main axis and by a regular sympodial branching pattern (fig. 190A). The second group is characterized by *T. gracilis* and *T. thesioides*. These species have minute and inconspicuous flowers arranged at the end of laterally short shoots and a main axis that grow on for several seasons (B). The growth form of all species is highly influenced by the orientation of the renewal shoots in space. The hypotonic and/or epitonic shoots are especially promoted. They are arranged subterminally in the first group ($C': R_{hy}, R_{ep}$) and in the medial zone of the SGU in the second (D: me). *T. hirtella* represents an intermediate condition between the two groups in having attractive flowers of medium size and a monopodial shoot connection.

The model of the genus *Thamnea* is shown in fig. 190A. The RS has a terminal flower surrounded by an involucre, a subfloral renewal zone and a branching zone with sylleptic vegetative and sylleptic flowering lateral shoots. The latter are mainly short and unbranched but able to continue growth in a sympodial manner. Variations of the RS (fig. 190B-D) illustrate the behaviour of the apex (B), that of the renewal shoots (C,C'), and the diversity of the branching zone (D).

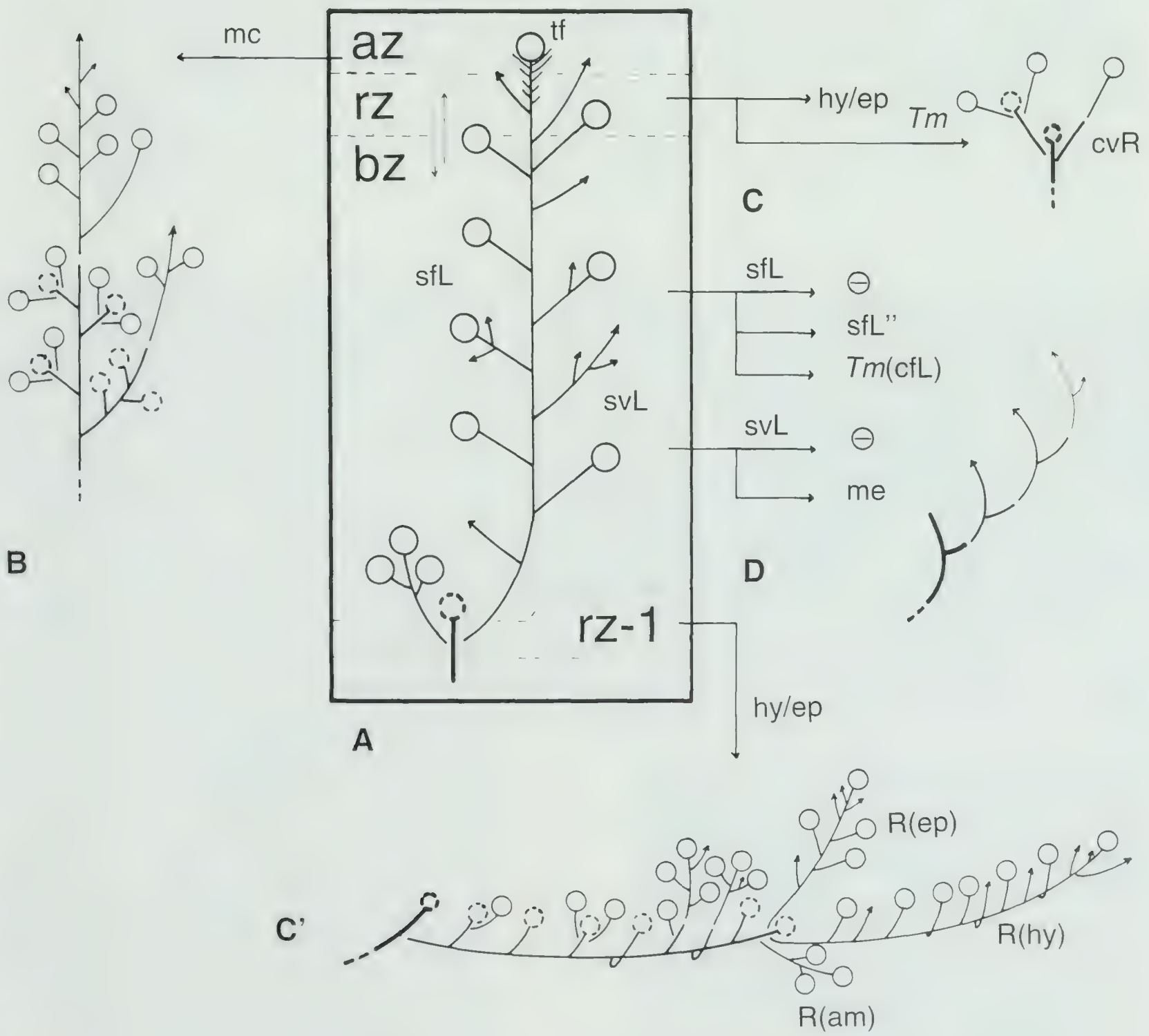


*Figure 190 - **Model of the genus* **Thamnea**. *A, reference system with terminal flower, subfloral renewal zone and sylleptic vegetative and flowering lateral shoots in the branching zone. B-D, variations of the model in respect of apex and mode of SGU connection (B: mc), behaviour of the renewal shoots relative to the time of development (C) and position (C'), variability of the branching zone (D).*

am, *amphitonic*, cvR, *cataleptic vegetative renewal shoot*, ep, *epitonic*, hy, *hypotonic*, *Tm*, *shifting in time.*

3.12 ***Tittmannia*** Brongn.

The genus comprised four species (Hall 1987b:62). T. esterhuyseniae *is known only from two localities one of which was visited in the company of Elsie Esterhuysen who first recorded its occurrence. It is situated on the privately-owned Overberg Farm `High Noon' at Kaaimansgat near Villiersdorp. A population of about eight large shrubs was present, within a Proteoid fynbos community below Stettynsberg. At a second nearby site several small plants were found to have resprouted from their lignotuber (fig. 3D).*

Only a few herbarium specimens of T. laxa *and* T. laevis *were available to the present study.*

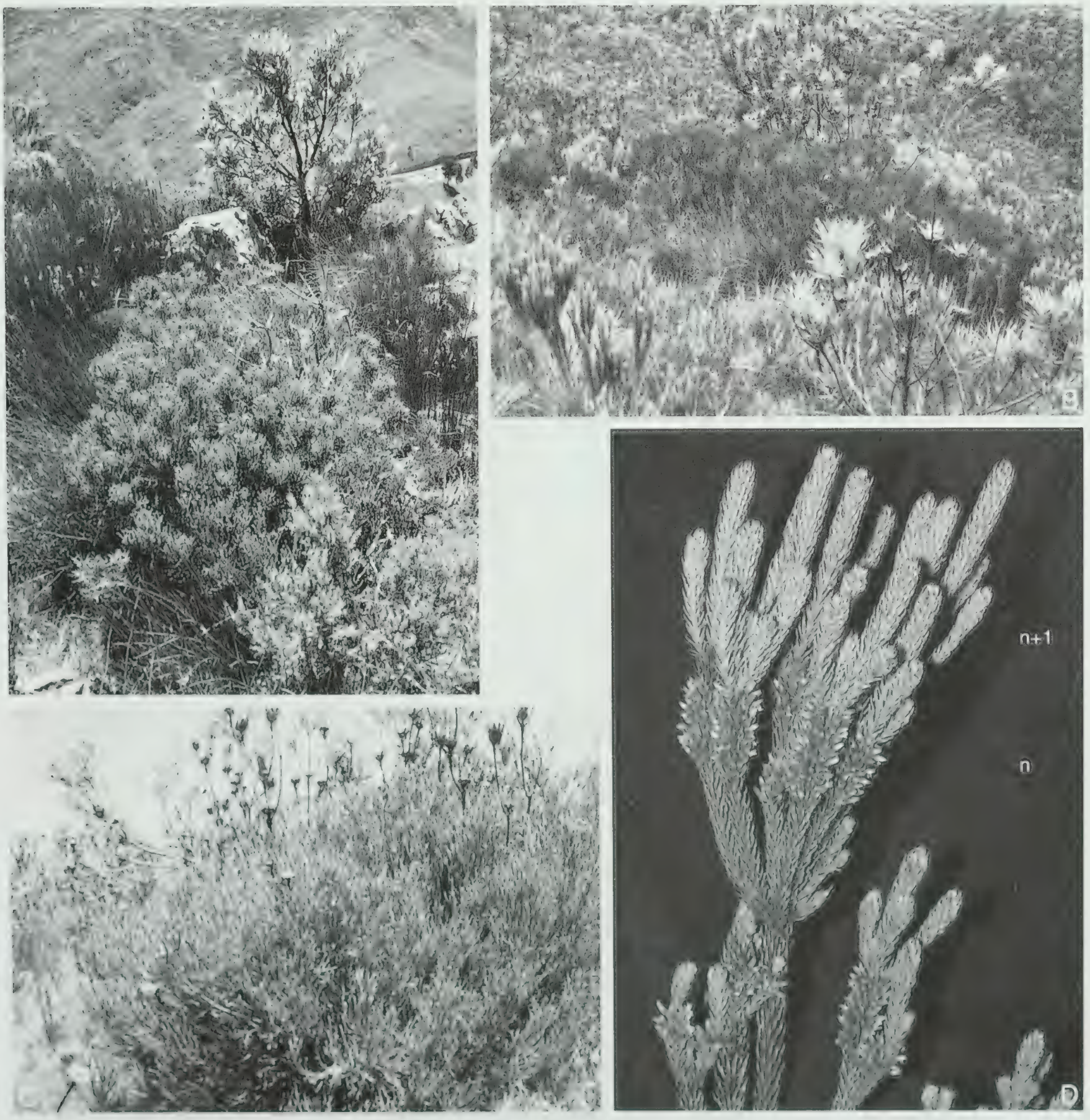


Figure 191 - **Tittmannia esterhuyseniae**. *A, shrub resprouted from the lignotuber, about 50 cm in height, B, C, shrubs within a Proteoid fynbos community, about two meters in height, D, flowering shoot system crowned by the already sprouted shoots of the next season.*

Growth and branching pattern. Shrubs of *T. esterhuyseniae* reach a height of about two meters (fig 191B,C). They exhibit a spreading growth form and are characteristically subdivided into a brown leafless centre formed by persistent leader shoots and a green, leafy and flowering periphery formed by the shoot systems of the last four seasons (fig. 191D, 193B). As with *Audouinia capitata*, each SGU forms a spike-like inflorescence in its distal region (fig. 192, 193). The apex remains indeterminate and is able to grow on for several seasons (mc). Thus, the individual sympodial unit is several seasons old. It comprises up to three SGUs which form a monopodially connected chain of shoots each of which has an inflorescence of a different age (n-1, n, n+1). After about three seasons the apex dies off and a new sympodial unit is formed by means of renewal shoots which arise above the subterminal inflorescence (R, rz). Besides the latter up to three sylleptic flowering lateral shoots (sfL) per SGU may appear, thus repeating the branching pattern of the dominant shoot. As they are of nearly the same length as the mother axis, flower simultaneously with it and are able also to continue terminal growth, the flowering periphery of the shrub is characterized by a regular branching pattern and an arrangement of the inflorescences in tiers (fig. 193B).

The simultaneous appearance of flowering and budding inflorescences is a characteristic feature of *T. esterhuyseniae* (Powrie 1969b: 363) and also of *Brunia nodiflora*. In both species the time of dormancy has been postponed, so that the usual pattern: vegetative stage, reproductive stage, dormancy has become a pattern in which the dormancy period occurs between bud formation and flowering. The result is that the next season's shoots and flower buds are already present (n+1) when the flowers of the current season begin anthesis (n). Fig. 191D shows the characteristic appearance of such a flowering shoot system, each of the spike-like inflorescences being crowned by a tuft of newly-sprouted shoots. In fig. 194 the branching and flowering behaviour of *T. esterhuyseniae* over four seasons is reconstructed schematically, summarizing at the same time the branching variability within the species.

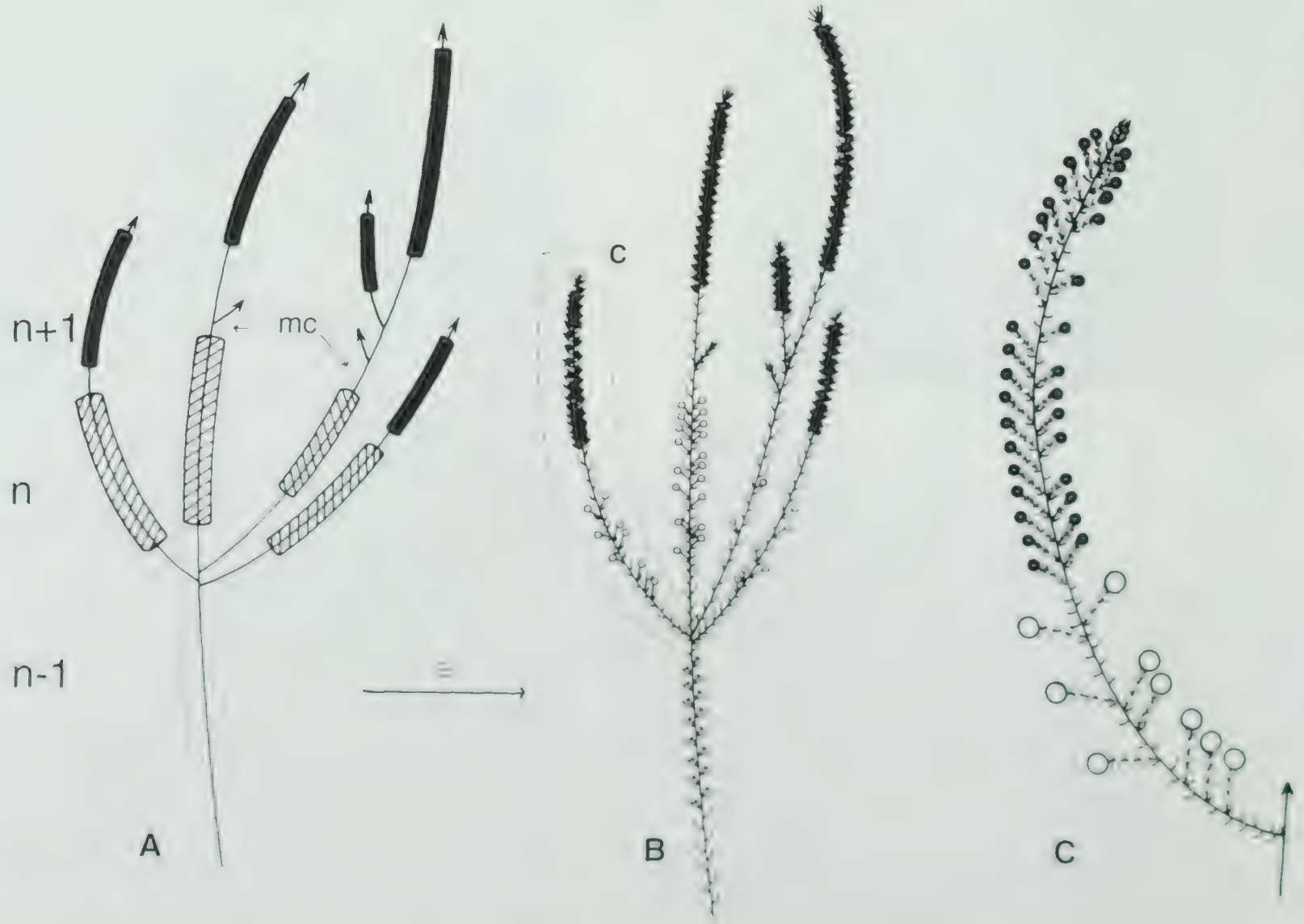


Figure 192 - **Tittmannia esterhuyseniae**. *A-B, profiles of a flowering shoot system showing the position (A) and organization (B) of the inflorescences, C, detail from B exactly showing all leaves, bracts and flowers.*

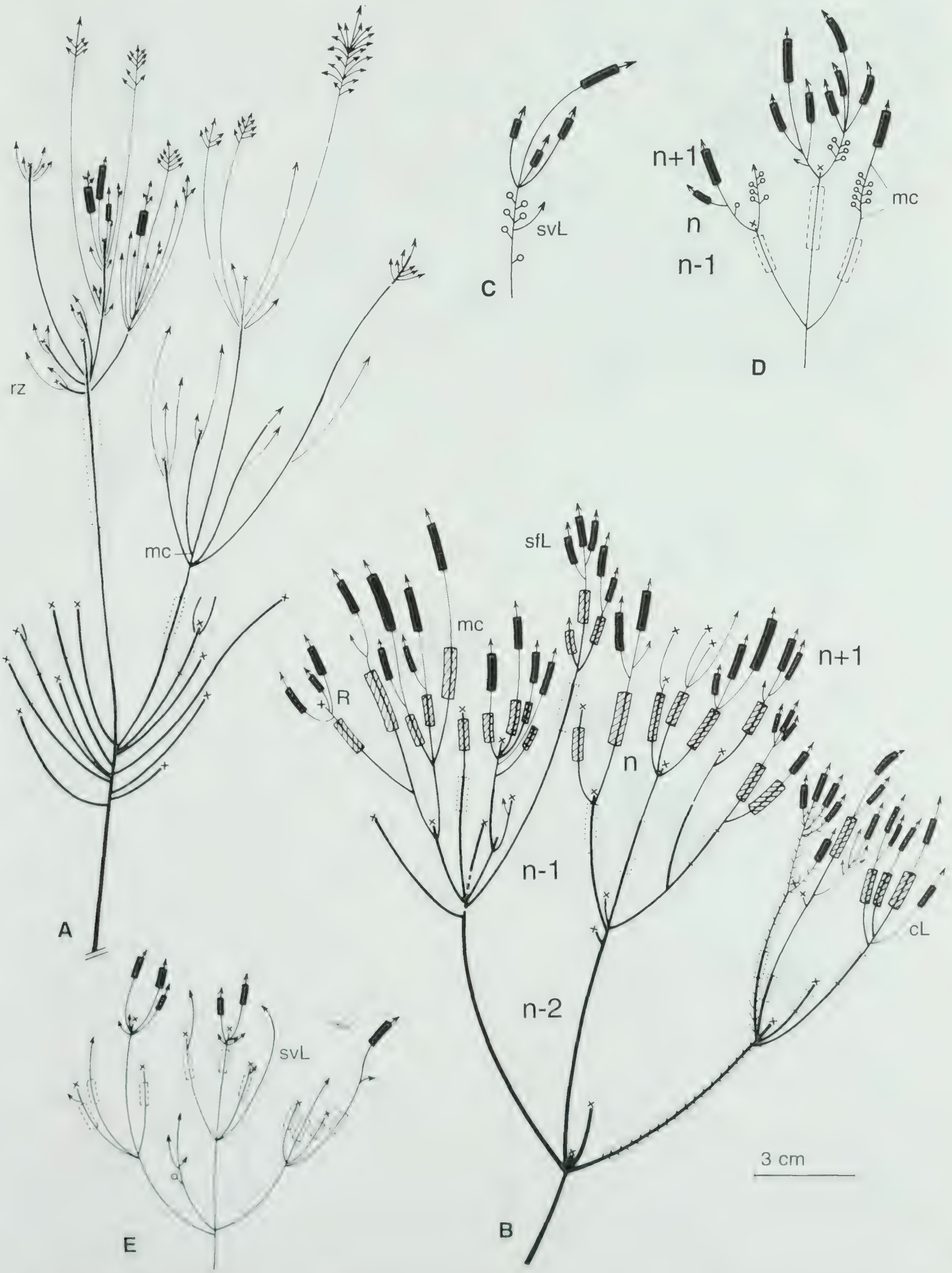


Figure 193 - **Tittmannia esterhuyseniae**. *Profiles of adult shoot systems: A, deflorated shoot system with much branched vegetative sprouters, B-E, flowering shoot systems showing the characteristic sympodial branching pattern of monopodially connected SGU-chains.* cL, *cataleptic lateral shoot.*

Though the branching pattern is in general very regular, it shows some variations. Occasionally individual lateral shoots grow out later (fig. 193: cL) or sylleptic vegetative lateral shoots appear below (fig. 193E: svL) or (rarely) among the flowers (fig. 193C: svL). In fig. 193A a shoot system is shown illustrating a change to juvenile growth behaviour. Above the deflorated inflorescences, much-branched shoot systems develop; these remain largely vegetative and possess long axes. The number of lateral shoots clearly increases (up to 10-15). Only two or three of them continue the shoot system, so that despite its high branching capacity, the shrub retains a slender and erect habit.

A similar pattern is noted in young shoot systems (fig. 195) which are only at commencing reproduction. The purely vegetative part is characterized by long, unbranched shoots connected mainly in a sympodial manner. It is clear that the apex of young vegetative shoots usually dies off after one season as opposed to the apex of flowering shoots which often continue to grow on terminally. The change in the shoot system from purely vegetative growth to reproduction is gradual. It is characterized by an increase in the number of both sylleptic flowering lateral shoots (fig. 195A: sfL) and renewal shoots (fig. 195A: rz), by the clear promotion of some individual renewal shoots (fig. 195A,B: R+) and by the increased monopodial connection of individual SGUs. The metamorphosis in shoot system is expressed in a change in plant habit, from a slender growth form to a more bushy structure.

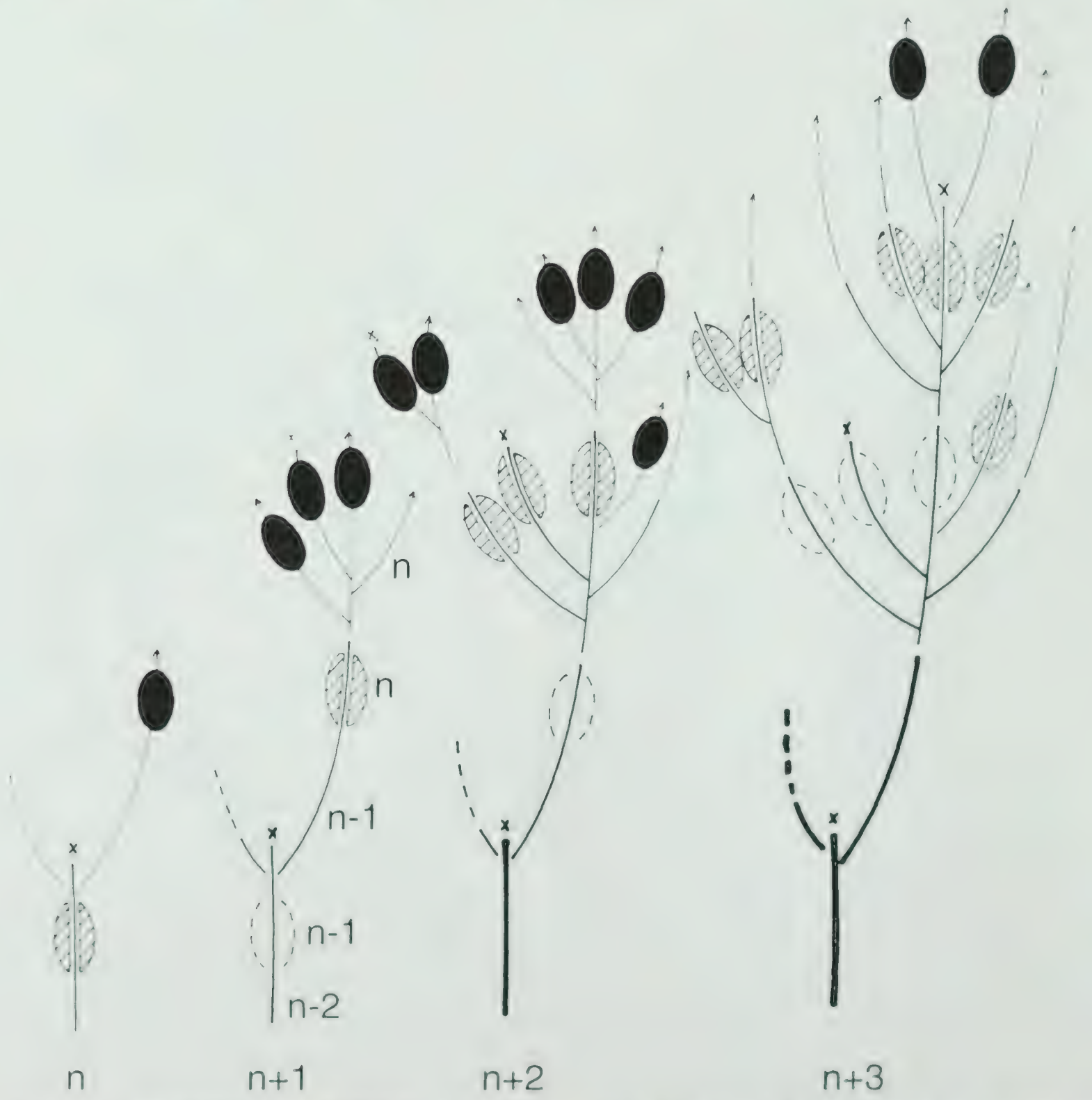


Figure 194 - **Tittmannia esterhuyseniae**. *Branching pattern of a flowering shoot system, four seasons old, schematically. Note that during anthesis (hatched) the next season's shoots and flower buds (black) are already present*

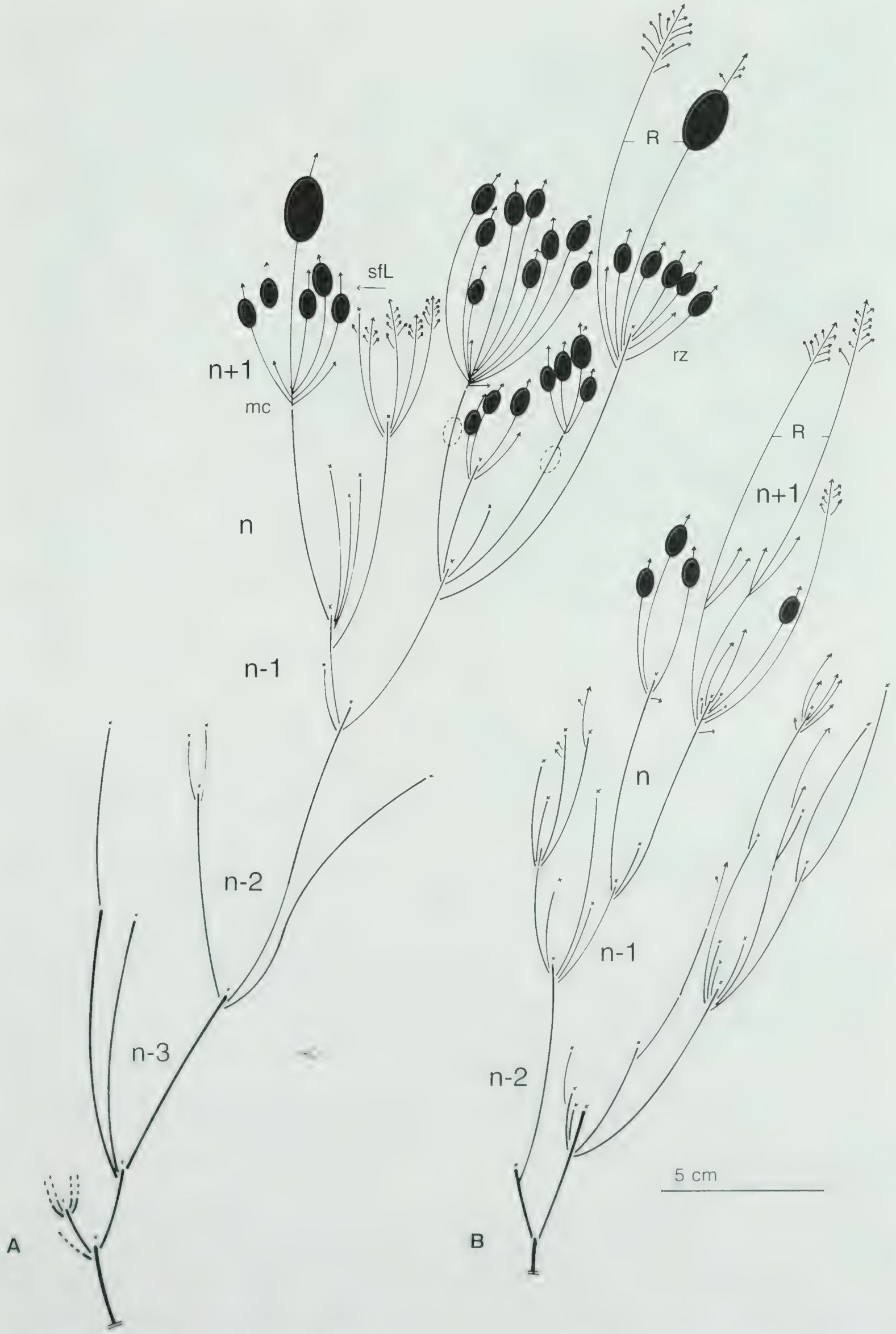


Figure 195 - **Tittmannia esterhuyseniae**. *A, B, profiles of young flowering shoot systems showing the change from the slender branching pattern of the vegetative shrub to the umbel-like branching pattern of the flowering shrub*

Figure 196 - **Tittmannia laxa.** *Flowering shoot systems (A, Compton 16093, NBG, B, Esterhuysen 28625, B).*

T. laevis and *T. laxa* (fig. 196) differ markedly from *T. esterhuyseniae* in appearance. Both species are low (to sixty centimetres high) shrubs with thin much branched shoots. Instead of the large spike-like inflorescences of *T. esterhuyseniae*, both species possess sparse inflorescences comprising about four (one to eight) individual flowers.

- The flowering shoot systems and profiles of *T. laxa* shown in fig. 196, 197A and 198 illustrate that the species has shoot systems of highly variable character. However, analysis shows that the underlying branching pattern is very uniform. It is characterized by a strong dimorphism between long leader shoots and much shorter flowering shoots. The renewal zone (fig. 197A, 198A: rz) has up to fifteen cataleptic lateral shoots. Usually two of these renew the shoot system and become long leaders (fig. 197A, A',198A: R+) while the remaining are much shorter and flower laterally. In the case of the leaders remaining largely unbranched, the regular branching pattern shown in fig. 196A and 198A results, while in the case of branched leaders the different length of the cataleptic shoots is masked by the lateral branch systems (fig. 196B, 197A).

  The leader shoots, if branched at all, have only indeterminate lateral shoots bearing flowering shoots of 2nd order of branches (fig. 198B: iL,II). These indeterminate shoots resemble the less promoted cataleptic shoots (fig. 197A: R-) whose developmental programme is thus repeated on branches of the 1st order.

  In general it is very difficult to identify the individual SGUs. The leaves persist and change only slightly with age. The deflorated inflorescences are only recognizable at the pedicels which persist in the axils of spread leaves. However, as the remaining leaves are appressed to the stem the zones of spread leaves mark the position of former inflorescences and thus allow identification of the individual SGUs. Both short-shoot systems, the less promoted cataleptic shoots and the sylleptic lateral shoots of the leaders, usually continue to grow on for two seasons until the apex dies off (fig. 197A: mc, B: n-2,n-1,n). A further branching is then possible only in a sympodial manner whereby the renewal shoots always arise above the uppermost flowers.

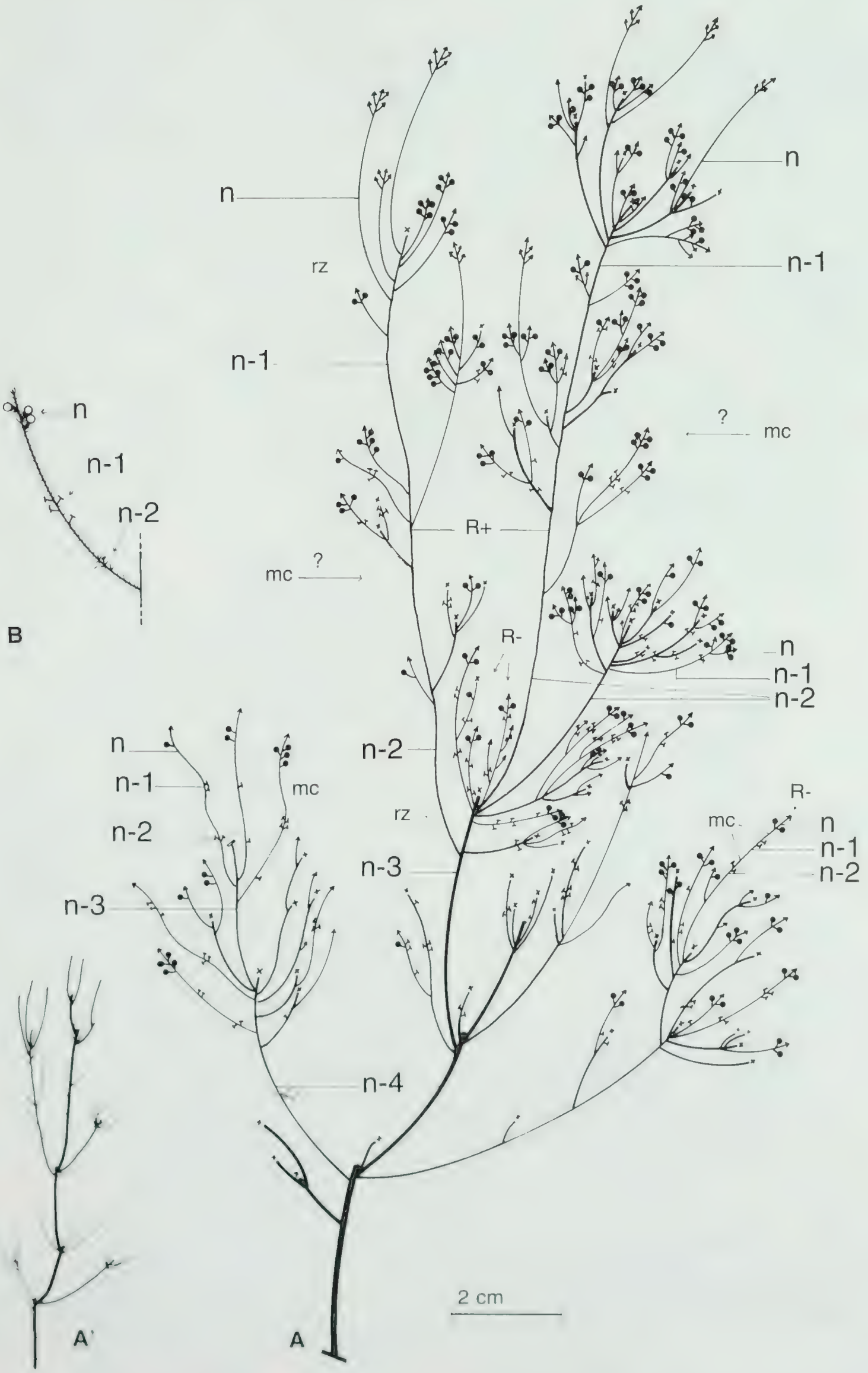


Figure 197 - **Tittmannia laxa**. *A', branching pattern and A, profile of a flowering shoot system (for the sake of clearness the flowers are shown black), B, detail of a lateral shoot, three seasons old, showing the foliage and the position of the flowers*

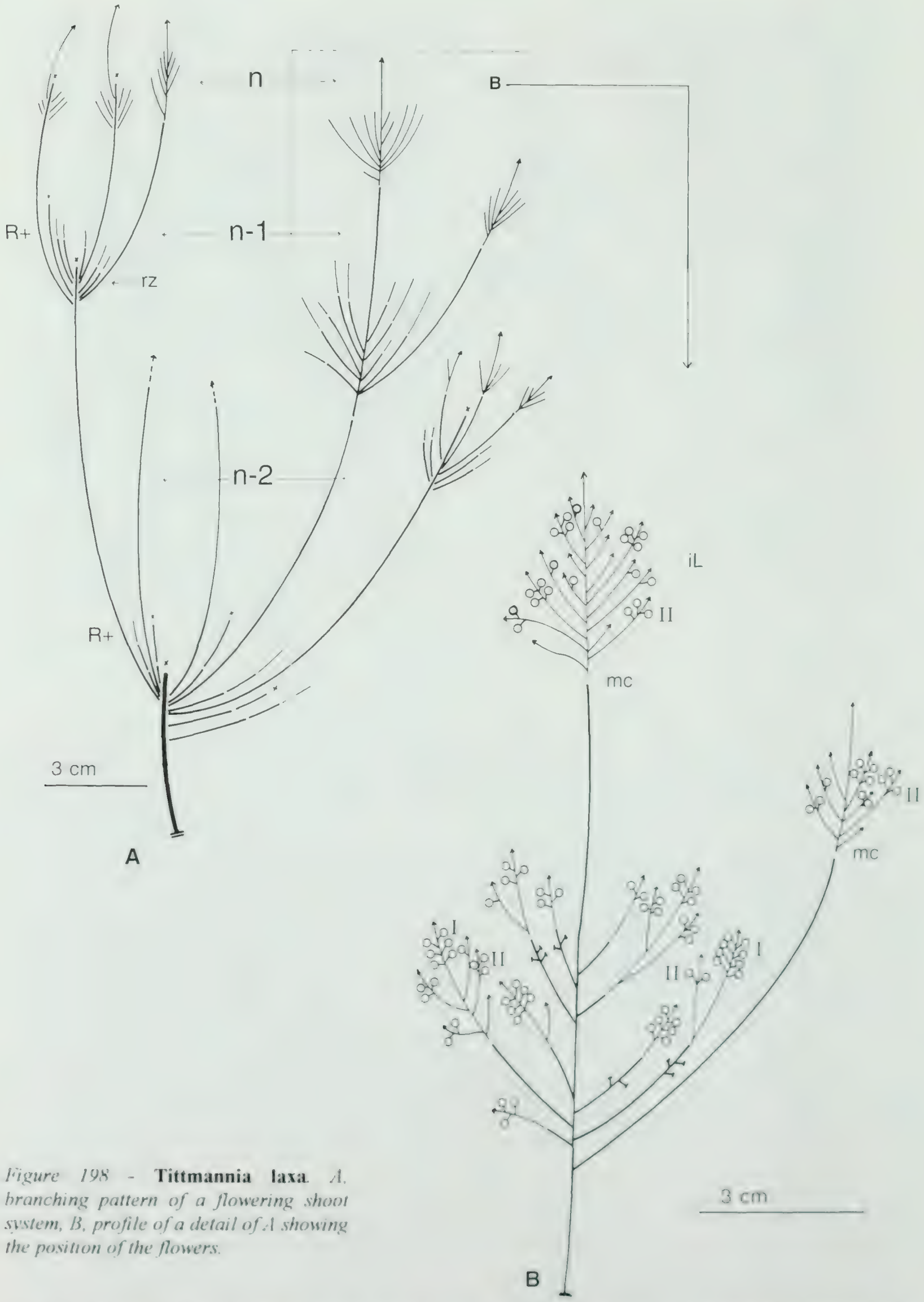


Figure 198 - **Tittmannia laxa**. *A, branching pattern of a flowering shoot system, B, profile of a detail of A showing the position of the flowers.*

It is probable that the leader shoots are also able to continue growth in a monopodial manner. The appearance of numerous lateral shoots in the central region of some leader shoots may indicate the new growth activity of the apex (fig. 197A: R+, 198A). Only on the supposition that the individual

leader shoots may age one season or more than one (mc) is it possible to predict with clarity the age of the overall shoot system (fig. 198A).

- The analysis of *T. laevis* remains very fragmentary because only two herbarium specimens were available for the present study. However, the profile in fig. 199 illustrates that the branching pattern is similar to that of *T. laxa*. In particular, leader shoots are found the short lateral shoot systems of which bear flowers and are able to continue terminally, as is the case with *T. laxa*.

Figure 199 - **Tittmannia laevis**. *Profile of a flowering shoot system.* cL, *cataleptic lateral shoot.*

A comparison of the branching patterns of *T. laxa*, *T. laevis* and *T. esterhuyseniae* shows that the three species are characterized by short flowering SGUs arranged in monopodially connected chains. The difference between the species (which at the same time influences the appearance of the shrubs) is caused by the equal or unequal length of the renewal shoots. In *T. esterhuyseniae* the spreading growth form of the shrubs is the result of a regular branching and the nearly equal length of all shoots. In contrast, *T. laxa* and *T. laevis* are characterized by a distinct shoot dimorphism between flowering short-shoot chains and long leader shoots which also bear flowering short-shoot chains laterally.

Leaf metamorphosis and inflorescence structure. The flowers are always laterally arranged terminating bracteate short-shoots (fig. 191D, 192, 200D). The five to eight bracts are clearly smaller than the leaves, but increase gradually in length in *T. esterhuyseniae* and *T. laevis* (fig. 200A-C).

In *T. esterhuyseniae* up to fifty densely aggregated flowering short-shoots form a spike-like inflorescence similar to that of *Audouinia capitata*. In both species vegetative shoots may appear within the flowering short-shoots (fig. 9A, 193C: svL). In *T. laxa* and *T. laevis* the flowers are not as densely aggregated, while sterile leaves and vegetative shoots appear among them more frequently. In summary it may be said that the inflorescences of *Tittmannia*, though they appear quite uniform in *T. esterhyuyseniae*, are not simple, indeterminate inflorescences but in fact (as in *Audouinia capitata*, *Linconia* sp. and *Pseudobaeckea teres)* solitary flowers at the end of bracteate short-shoots.

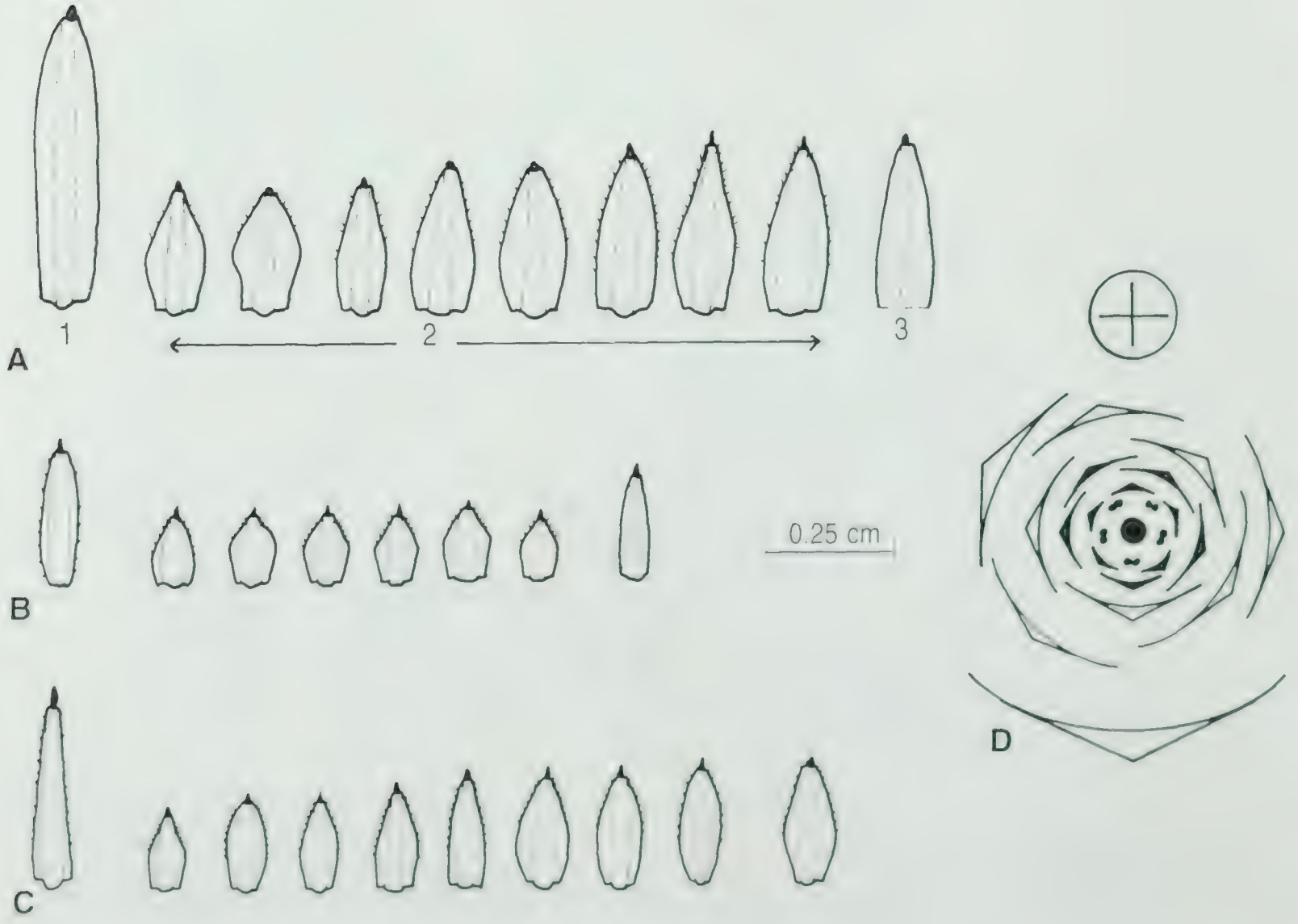


*Figure 200 - **Leaf metamorphosis in the genus* Tittmannia. *A*, T. esterhuyseniae, *B*, T. laxa, *C*, T. laevis, D, *diagram of a flowering short-shoot. 1: flower-subtending leaf, 2: flower surrounding bracts, 3: sepal*

Summary. The branching pattern and flowering behaviour of the genus is summarized in fig. 201. The RS (A) shows an indeterminate apex, a subterminal renewal zone and a branching zone with sylleptic flowering bracteate short-shoots in its distal zone (sfL). Sylleptic vegetative shoots and sylleptic flowering lateral shoots repeating the main axis, may additionally appear in the proximal region.

All species demonstrate monopodial shoot connections (B). *T. esterhuyseniae* is characterized by a shifting in time (*Tm*), resulting in synchronization of the anthesis of season n and bud formation of season n+1 (B',C). In *T. laxa* and *T. laevis* a shoot dimorphism characterizes the habit of the shrubs. It is primarily the result of an unequal promotion of the renewal shoots (C'). The leader shoots never provide a subterminal cluster of flowering short-shoots, but bear only indeterminate lateral shoots flowering at the end of branches of 2nd or 3rd order (D').

The bracteate nature of the flowering short-shoots and the appearance of sterile leaves and vegetative shoots among the flowers (D) lead one to the conclusion that the genus does not have simple indeterminate inflorescences but in fact more or less densely aggregated solitary flowers at the end of lateral short-shoots.

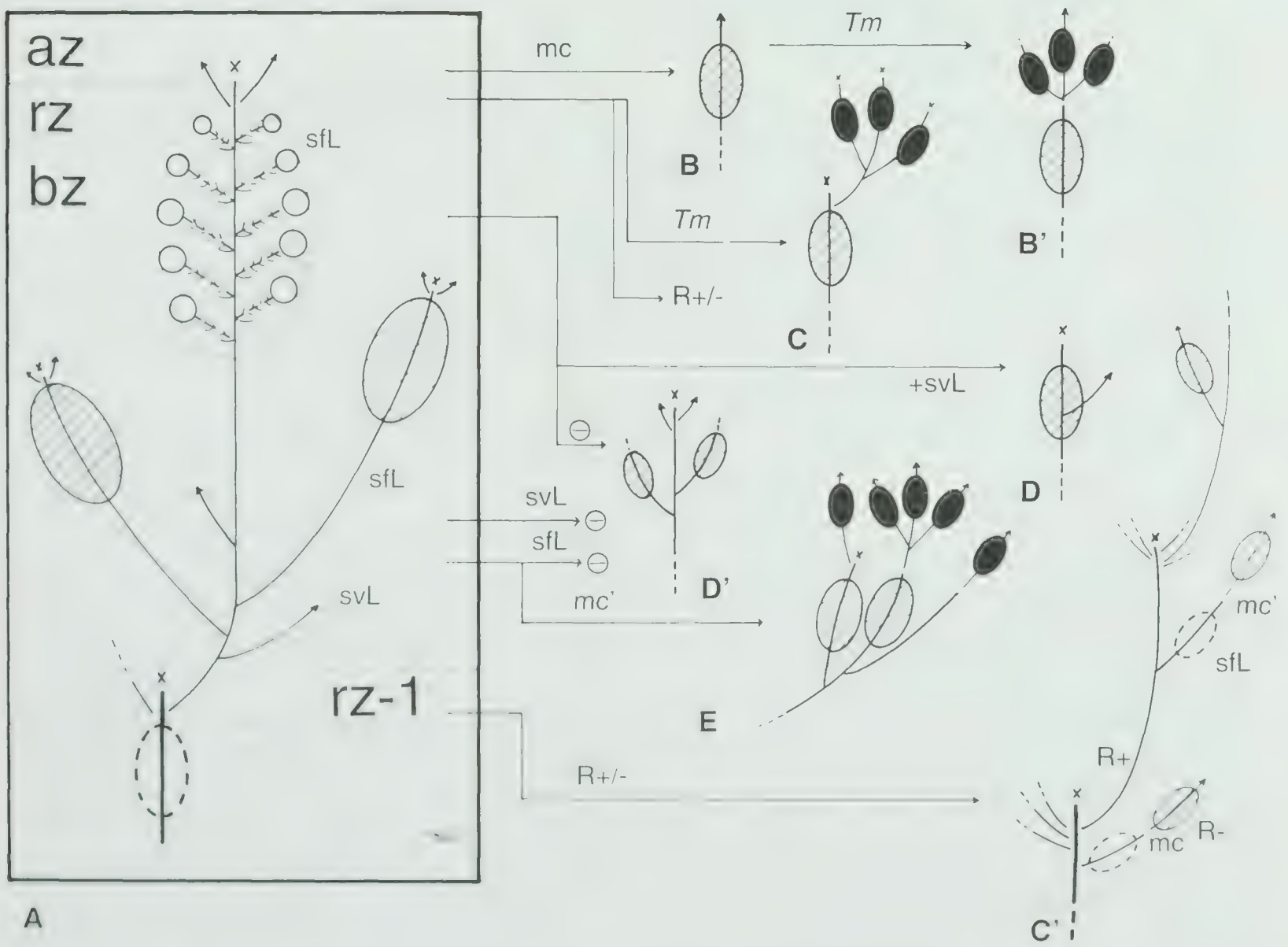


*Figure 201 - **Model of the genus* **Tittmannia**. *A, reference system (RS) showing the indeterminate apex, the subterminal renewal zone and the branching zone with flowering short-shoots in the distal and sylleptic vegetative and flowering lateral shoots in the proximal zone. B-E, variations of the RS in respect of apical activity (B), the shifting in time between two succeeding SGUs (B',C), the unequal promotion of renewal shoots resulting in shoot dimorphism (C'), the habitual uniformity (D) and lack of the 'subterminal inflorescence' (D') and the behaviour of the lateral flowering shoots (E). Tm, shifting in time.*

4

Inflorescences in woody plants

The high structural and positional diversity of inflorescences demands a typology which not only provides a survey of the various forms, but above all brings identities to light. The concept of synflorescences set up by Troll (1964, 1969) represents such a general reference system. However, its application to woody plants is not undisputed. The present chapter summarizes the basic questions in comparing inflorescences in woody plants (§4.1) and reviews both the concept of Troll and alternative approaches provided by 20th century plant morphologists (§4.2). Subsequently the reference system applied to the Bruniaceae is explained and tested against other plant groups (§4.3).

4.1 Basic questions in comparing inflorescences in woody plants

4.1.1 The example of the Bruniaceae

The morphological analysis of the Bruniaceae has shown that both structure and position of the flowers are highly diverse within the family. Solitary flowers in a terminal and/or lateral position appear in *Thamnea* and *Mniothamnea*. Spike-like inflorescences on a protruding main axis are found in *Audouinia*, *Linconia* and *Tittmannia*. Head-like aggregates of only a few or up to several hundred flowers characterize the genera *Brunia, Berzelia, Nebelia, Raspalia, Pseudobaeckea, Staavia* and *Lonchostoma*. They are arranged terminally and/or laterally, have a terminal flower or not, appear solitarily or in aggregates and show a globose, pincushion- or strawflower-like appearance.

Figure 202 summarizes the diversity in Bruniaceae and points to the difficulties which arise in trying to compare the different species morphologically.

(1) The flowering shoot system of *Staavia glutinosa* (A) comprises four seasons growth (n-3 - n). The shoot system is regularly branched in a sympodial way, that is a sympodial unit (SU) is formed in each season, thus corresponding to a seasonal growth unit (SGU). The SGU is subdivided into a terminal inflorescence (ti), a subfloral renewal zone (rz) and a remaining unbranched shoot. The renewal shoots do not develop before the next season and thus show a cataleptic behaviour relative to their parent axis.

(2) *Raspalia globosa* (B) also shows a regular sympodial pattern, but the renewal shoots start to sprout sylleptically, that is in the same season in which their parent axis has been formed (sR). Besides the terminal inflorescence (ti), additional lateral inflorescences appear at the end of sylleptic flowering lateral shoots (sfL). Comparing the two species *Staavia glutinosa* and *Raspalia globosa* the question arises: which flowering parts are comparable to each other? In answering the question it becomes necessary to distinguish between strictly descriptive terms e.g. 'inflorescence' and typological terms which permit recognition of identical units. In the present paper, flowers and inflorescences of different species which are supposed to be comparable (morphologically 'homologous') to each other are termed 'reproductive units' (RU). Thus, the question reads: which is the RU in *Raspalia globosa*, each individual head-like inflorescence or all inflorescences of an individual SGU together? Is the terminal inflorescence in *Staavia glutinosa* comparable to the terminal inflorescence in *Raspalia globosa* or to the terminal inflorescence and all sylleptic flowering lateral shoots together?

(3) *Brunia albiflora* (C) has only lateral inflorescences. The apex of the main axis remains active and continues to grow on in the next season. Thus, the SGUs concerned are connected in a monopodial way (mc). Looking at a several season old shoot system (fig. 63), it becomes clear that this species is also sympodially branched, but in a superior manner. The individual SU corresponds to a shoot chain composed of several monopodially connected SGUs (MU).

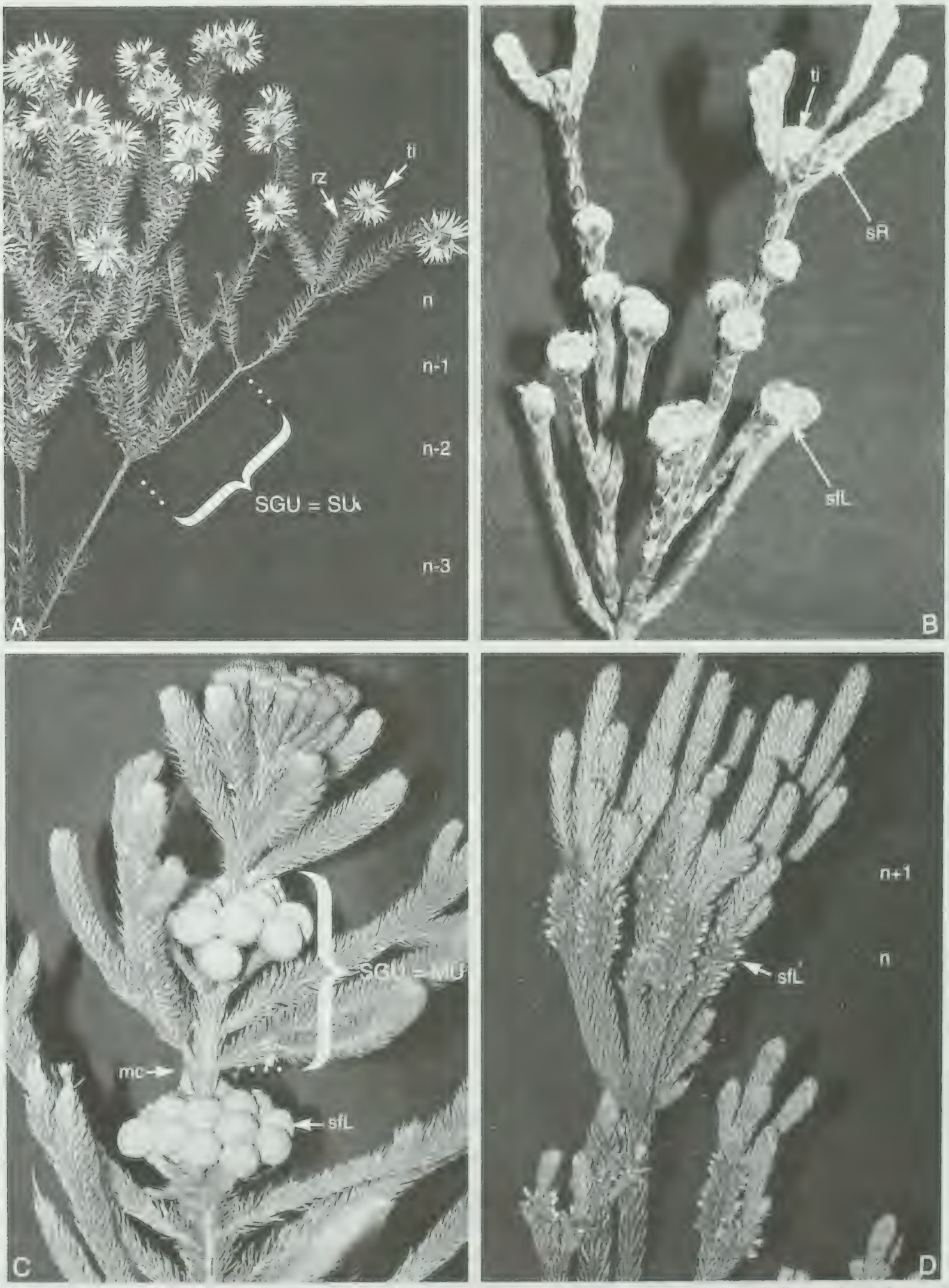


*Figure 202 - **Bruniaceae.** Appearance of flowering shoot systems. A,* Staavia glutinosa, *B,* Raspalia globosa, *C,* Brunia albiflora, *D,* Tittmannia esterhuyseniae. sR, *sylleptic renewal shoot*

In Bruniaceae (as in many other arborescent species) the identification of the individual SGUs is occasionally difficult because the usual criteria: seasonal leaf loss, bud formation, internodial curve and leaf metamorphosis are not applicable to the family. The only information regarding the age of an individual shoot system is given by the gradual ageing of the inflorescences (bud, flower, fruit, leaf scars) and leaves. The latter usually persist for three or four years in Bruniaceae, changing their texture with time. Young leaves are softly hirsute and fresh green, older leaves tend to become

glabrous, hard and dark-green, while old leaves are brownish and are gradually shed. With the help of the different ages of inflorescences and leaves, it can be seen that the individual SU of *Brunia albiflora* comprises up to five SGUs (see fig. 63).

(4) *Tittmannia esterhuyseniae* (D) shows a similar branching pattern to *Brunia albiflora*. However, individual flowers not inflorescences are laterally arranged around the main axis. Each of the individual flowers terminates a bracteate short-shoot (sfL). Besides, the apex of the main axis and the renewal shoots start to grow extremely early. The buds of the next season's flowers (n+1) are already formed when the flowers of the present season (n) are at anthesis. Again the question arises: Which unit corresponds to the RU: the entire spike-like inflorescence in *Tittmannia esterhuyseniae* and the whole aggregate of lateral inflorescences in *Brunia albiflora*, or each of the individual flowers and inflorescences laterally arranged round the protruding main axis?

In a more generalized way, the morphological analysis of the structure, position and development in time of the inflorescences in Bruniaceae results in two main questions:

(1) Which part of the flowering shoot system should be recognised as the reference system (RS) for the comparison of flowering woody plants?

(2) Which part of the reference system corresponds to the reproductive unit (RU) of the species concerned?

4.1.2 The problem of finding an appropriate reference system

The first question deals with the conventional approach of taking the SGU (or a comparable unit of time) as reference system (e.g. Pilger 1922, Troll 1964, Briggs & Johnson 1979). However, as fig. 203 illustrates, the SGU in Bruniaceae is not necessarily the most appropriate RS.

The shoot systems of e.g. *Lonchostoma* and *Staavia* show a regular sympodial branching pattern (A). However the pattern of organization does not correspond to the pattern in time. Two sympodial units (SU) may appear within one season (n) by sylleptic development of the renewal shoots (a). The sympodial unit may age several seasons by inserting monopodial units (b). The development of the sympodial unit may begin in one season and finish in the next (c). Because of the high variability in time, individual SGUs of the sympodial branching pattern are very different and the SGU is not an appropriate RS in these systems.

In contrast, the shoot systems of e.g. *Berzelia* and *Audouinia* (B) show no marked variation in time. But, though the individual SGUs look very similar, they are in fact not comparable. In the case of monopodial shoot connection (mc) the apex continues to grow on, while in the case of sympodial shoot connection (sc) the apex dies off, the system being renewed by lateral shoots (rz). Only by ignoring this difference, may the SGU be taken as RS in these shoot systems.

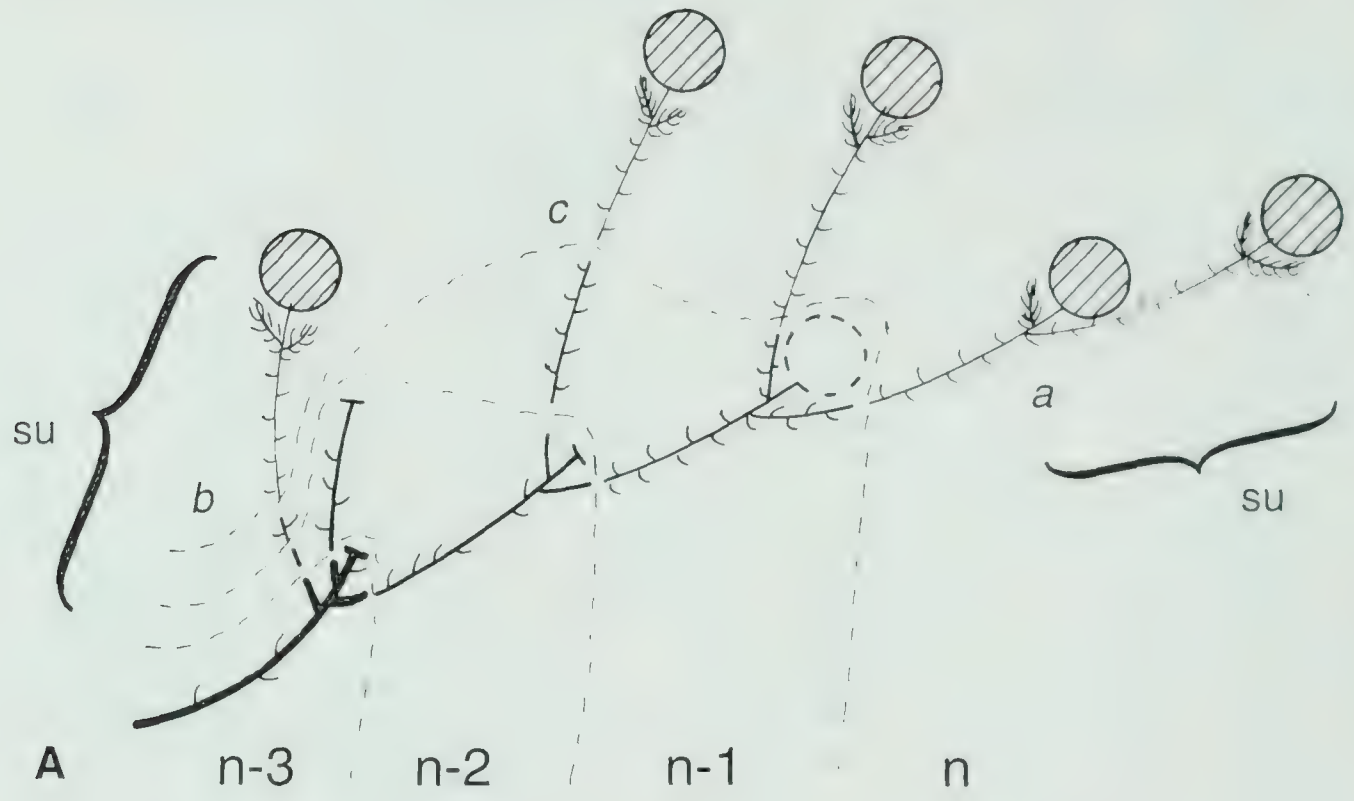
Summarizing, some branching patterns are better characterized by their organizational pattern, that is the SU in case of the Bruniaceae (A), and others by their pattern in time, that is the SGU (B). Neither of the patterns alone qualifies as a general reference system for the comparison of flowering shoots in Bruniaceae.

4.1.3 The problem of finding the reproductive unit

The second question deals with the definition of the individual reproductive unit and thus with the problem of deliminating inflorescences in woody plants. Figure 204 illustrates the problem in the Bruniaceae.

Audouinia (A) has a divergent flowering spike-like inflorescence with individual flowers, each of which is surrounded by 8-16 bracts. The main axis of the inflorescence continues to grow on and dies off after several seasons. The shoot system is renewed by lateral shoots arising above the inflorescence (rz).

Berzelia (B) has only lateral inflorescences. They are arranged in a raceme or double raceme and flower in a basipetalous sequence. Each of the individual inflorescences terminates a relatively short bracteate shoot. It ends in a terminal flower which is often the first one to flower while the remaining flowers show a divergent flowering sequence. Each of the axillary flowers has a subtending bract and two prophylls. As in *Audouinia* the main axis of the flowering shoot system continues to grow on and is finally renewed by shoots arising above the flowering zone.



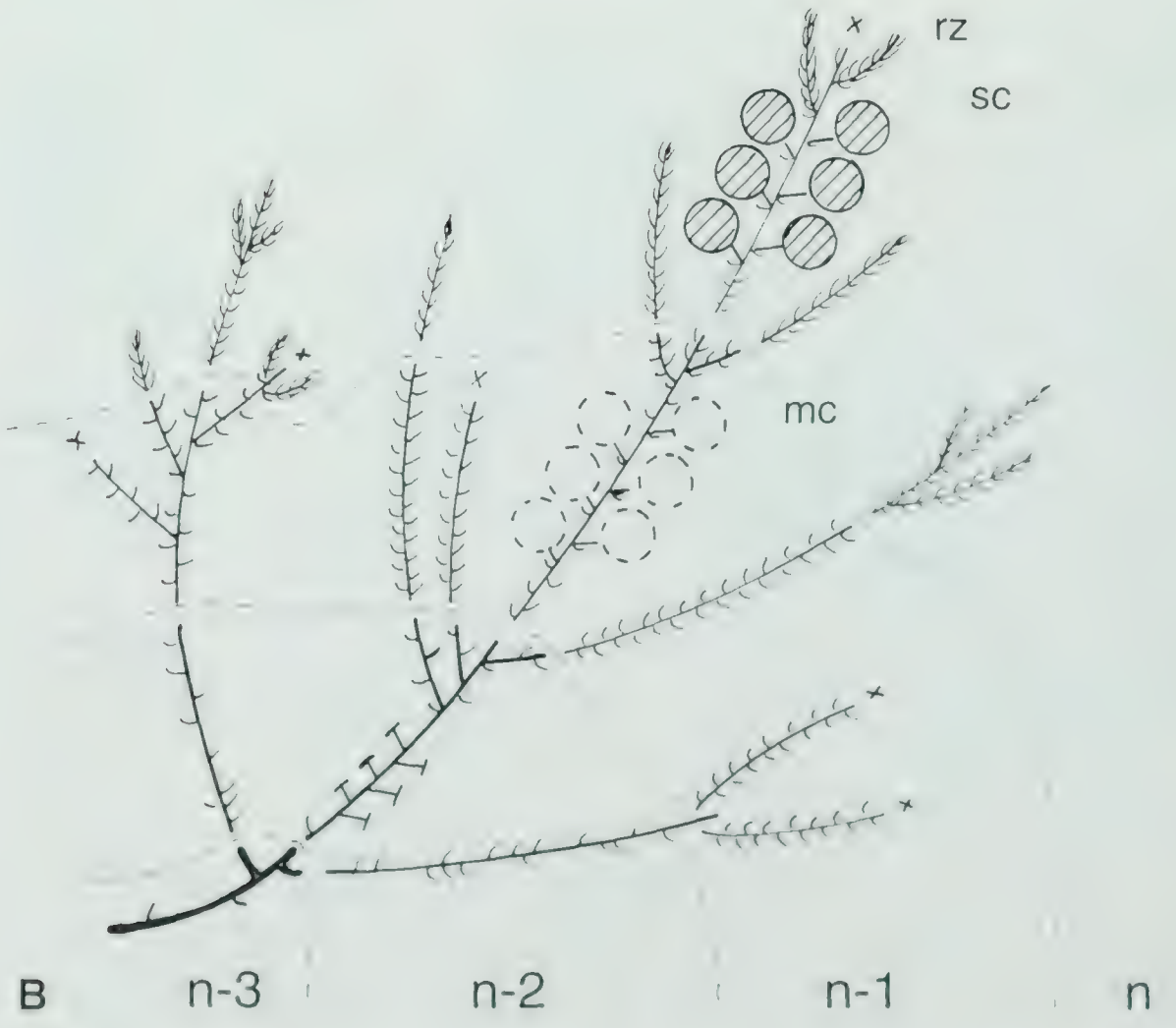


Figure 203 - ***Shoot systems in Bruniaceae,*** *schematically. Note that the regular patterns are formed by sympodial units in A and by similar SGUs in B. Both examples show that the SUs do not correspond to the SGUs. a, accelerated development of SUs, b,c, retarded development of SUs*

Raspalia (C) comprises species which have both lateral and terminal inflorescences with the renewal zone in between. The individual inflorescences show a terminal flower in some species and are truncate in others. Each of the axillary flowers has a subtending leaf and two prophylls. The flowering sequence is highly variable.

Lonchostoma (D) is largely characterized by terminal indeterminate inflorescences. Each of the axillary flowers has a subtending leaf and two, rarely three `prophylls´. Forced by the terminal inflorescence the branching pattern is sympodial, with renewal shoots arising below the inflorescence.

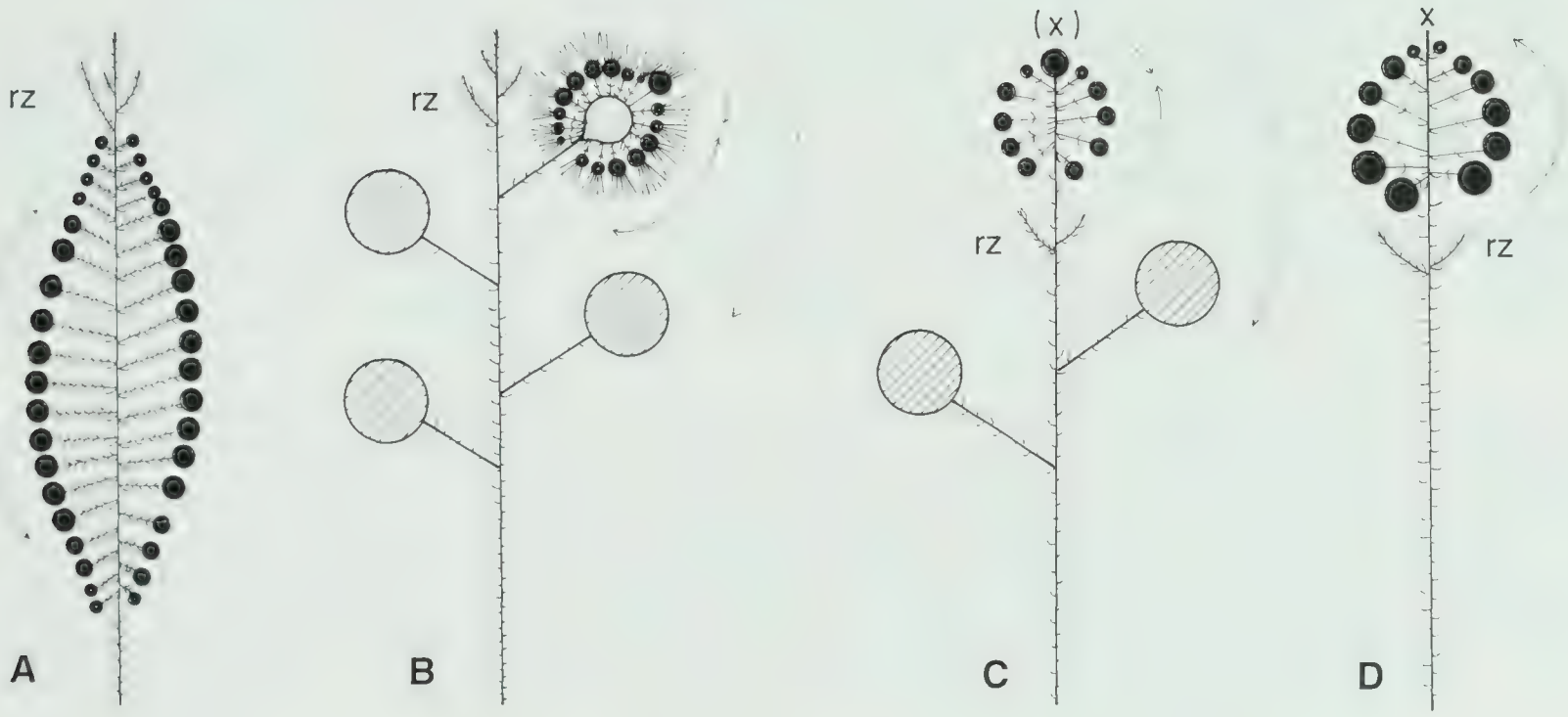


*Figure 204 - **Inflorescences in Bruniaceae and the question of homology**. A-D, profiles of the inflorescences in* Audouinia capitata *(A),* Berzelia arachnoidea *(B),* Raspalia globosa *(C) and* Lonchostoma purpureum *(D). E, comparison of the inflorescences. Note that dependent on the definition of the reproductive unit there are three different possibilities to homologize the inflorescences to each other (1-3). Compare with text. Arrows in A-D: flowering sequence; (x) in C: terminal flower present or absent.*

Comparing the inflorescence of *Audouinia capitata* with the remaining inflorescences (E) different definitions of the reproductive unit are possible, each resulting in a different homology:

(1) The RU corresponds to all flowers formed in one season (cross hatched). The whole spike-like inflorescence in *Audouinia* is comparable to the sum of all inflorescences per season in *Berzelia*, *Raspalia* and *Lonchostoma*.

(2) The RU corresponds to each of the individual clearly separated inflorescences (hatched). The whole spike-like inflorescence in *Audouinia* is comparable to each of the lateral and/or terminal inflorescences forming individual units in the remaining species

(3) The RU corresponds to each of the strictly reproductive not persisting parts of the shoot system (black). The individual lateral flowering short-shoot in *Audouinia* is comparable to each of the lateral and/or terminal inflorescences in the remaining species.

This short example illustrates that a clear definition of the reproductive unit is urgently required. There is a need to assess whether one of the criteria listed above (time of development, individuality, quality) is able to define the RU or whether further aspects have to be taken into consideration.

4. 2 A short history of morphological concepts and disputes

The predominantly descriptive attempts at analysis and classification of the many known inflorescence types (see Celakovsky 1893, Parkin 1914, Rickett 1944, 1955, Zimmermann 1965) were followed by the typological concept of synflorescences introduced by Troll (e.g. 1964b, 1969b). This concept for the first time permitted comparison and homologization of the inflorescences of different species regardless of their appearance and foliage and thus was the basis for using inflorescence characters for systematic purposes (compare with Weberling 1963, 1971). The rapidly increasing knowledge about inflorescences illustrated the degree of variation of the Trollian types and resulted in the formulation of elementary guidelines to characteristic evolutionary tendencies in inflorescences (e.g. Maresquelle 1970, Sell 1976). However, the deficiencies of the Trollian concept became clear as well. The elaborate terminology, the interpretation of indeterminate synflorescences and particularly the application of the concept to woody plants, were all criticised (e.g. Briggs & Johnson 1979, Schröder 1987, Kunze 1989.)

The following survey of morphological concepts is far from being complete. Rather it summarizes selected references dealing with fundamental questions of inflorescence morphology and particularly with inflorescences of woody plants. Individual examples are illustrated in more detail to elucidate the view of the authors concerned. As regards the figures, data are taken from the papers cited. However, the figures themselves might be slightly changed, simplified or even completely new, being explained by 'modern' terms compared with the original publications. The numerous comments reflect the personal view of the author, who has been engaged in the study of inflorescences for more than fifteen years.

4.2.1 Inflorescences and woody plants: early concepts

In the beginning of the 20th century foliage played an important role in defining inflorescences. Goebel (1931) for example distinguished 'inflorescences' (flowering shoots with a foliage different from the vegetative part), 'flowering sprouts' (flowering shoots with a foliage not different from the vegetative part) and 'anthoclades' (flowering shoots alternately bearing leaves and flowers). Both Parkin (1914) and Pilger (1921,1922) defined an inflorescence as a bracteate flowering shoot system being separated from the vegetative part of the plant by the altered foliage. But as this criterion was insufficient they tried to explain transitional forms by reconstructing the evolution of the inflorescences. In doing so the authors developed two different concepts.

4.2.1.1 The concept of Parkin. Parkin (1914) held the opinion that all kinds of inflorescences arose from a single terminal flower. In doing so he distinguished two different modes of evolution:

The first (fig. 205A-E) begins with a shoot system bearing a flower at the end of the main axis (A: tf). This flower is gradually enriched (*En*) by axillary flowers in a basipetalous sequence (B-C). The result may be a terminal bracteate determinate inflorescence (D). Indeterminate inflorescences (E) then result from inhibition of the terminal flower (*I*). According to Parkin, this mode of production of axillary flowers represents the most common means by which inflorescences are formed.

The second mode (fig. 205F-I) is termed segregation. It begins with a sylleptically branched shoot system that bears individual flowers at the end of each of the leafy lateral shoots (F: tf). The apex of the main axis remains open and continues to grow on. As the individual flowers are separated from each other by foliage, each is taken as a terminal flower equivalent to the terminal flower of the main axis (A). Like the latter, each may be enriched by axillary flowers forming a separate inflorescence (compare with A-E). But it is also possible that all flowers - after aggregation of the originally separated flowers (*A*) and reduction of the leaves (*Rfo*) - form a superior flowering unit (F-H) which is borne on the main shoot. Parkin introduced the term 'intercalary inflorescences' (in) for these forms. Finally, when the apex of the intercalary inflorescence becomes inhibited (*Iap*), a terminal bracteate indeterminate inflorescence results (I) which is however, despite its same position and structure, analogous to that which has arisen by truncation of the terminal inflorescence (E).

According to Parkin the formation of inflorescences always begins at the apices of the shoots concerned. Consequently, he ignored both life and growth form of the plants and listed examples of both herbal and woody plants.

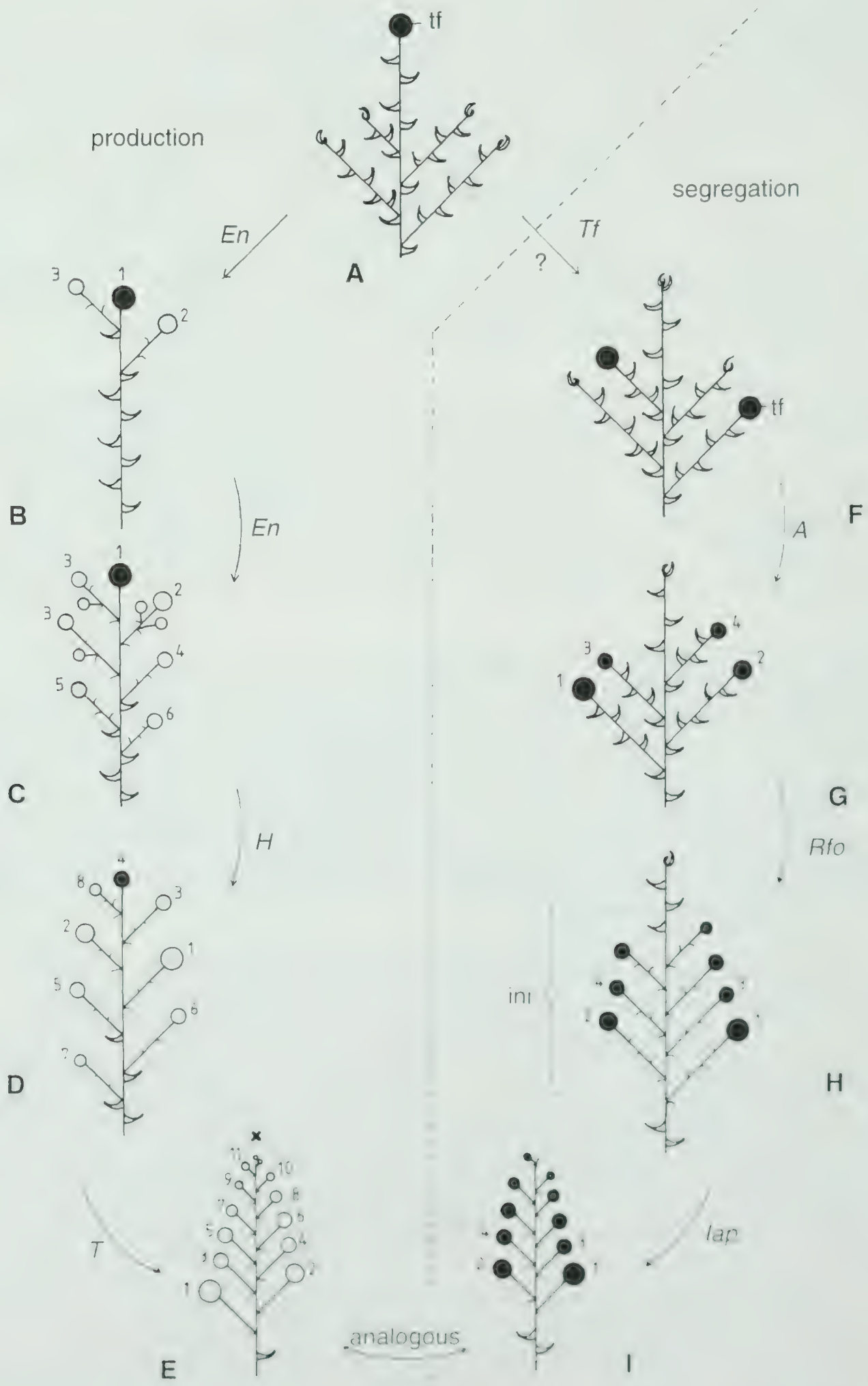


*Figure 205 - **Evolution of inflorescences after Parkin (1914)** showing inflorescences arising from individual terminal flowers (A, F) either by production (A-E) or by segregation (F-I).*
Redrawn after Parkin (1914), simplified and slightly changed; compare with text.
A, aggregation, lap, inhibition of apex , ini, *intercalary inflorescence, Rfo, reduction of foliage, Tf, transformation (some terms originate from the mid of the century, and are included here for greater clarity).*
black: terminal flower, white: axillary flowers enriching the terminal flowers

Parkin attached importance to the growth form only insofar as it related to the intercalary inflorescences of woody plants. He argued that trees and shrubs might be handicapped by flowering terminally before longitudinal growth had been completed and that these plants therefore `transferred´ the production of flowers onto lateral shoots. *"The tree or shrub can thus continue its upward vegetative growth without at the same time deferring its flowering"* (1914:549).

Obviously he took the determinate shoot system (A) for the original state and the process of segregation for an advanced stage. But he did not derive the latter from the first by truncation (as is suggested by the reconstruction of Parkin´s theory by Weberling, 1992:30), but rather pointed several times to the independence of the two parallel evolutionary ways: *"Reasons are adduced for regarding these two main classes of inflorescences as not being strictly comparable to each other, since their respective evolutions commence differently. An apical inflorescence arises from a single axis bearing a solitary terminal flower. An intercalary inflorescence requires two or more of such axes for its evolution. An apical inflorescence is produced by the pushing out of new flowers alongside the terminal one. An intercalary inflorescence, on the other, results when a number of adjacent lateral axes bearing terminal flowers lose their foliage and shorten their internodes. The one is a new production: the other a segregation."* (1914:560)

What Parkin really meant by `transfer´ of flower production from the main shoot onto lateral shoots is open to speculation. Perhaps he used the term because he first studied inflorescences of herbal plants and only later those of shrubs and trees. Perhaps he was ahead of his time and implied something like homeotic genes causing flowers to develop at different positions. However, it must be noted that Parkin did distinguish two independent evolutionary pathways to the formation of inflorescences, not directly derivable from each other.

4.2.1.2 The concept of Pilger. In contrast to Parkin, Pilger (1921, 1922) focused upon the whole plant and thus had to attach importance to its growth form. As regards woody plants he discussed the particular difficulties which arise in analysing flowering shoots of woody plants. He took the sylleptically branched (in his terminology: proleptic) shoot system of tropical woody plants to be the basal condition and the unbranched annual shoots, the renewal buds and the seasonal leaf loss of the temperate woody plants to be derived. Consequently, Pilger disapproved of the term `Jahrestrieb´ (annual shoot) which only relates to temperate climates and proposed the terms `Jahresabschnitt´ (part of an annual shoot) or `Schub´ (push) to include lammas shoots (`Johannistriebe´) as well as seasonal shoots of other climates. Pilger took the unbranched `Schub´ as basis for his own studies and thus was one of the first to explain his frame of reference.

Pilger did not illustrate his theory of inflorescences, but a reconstruction of his view is attempted here (fig. 206). As regards woody plants, the vegetative shoot system is formed first (A) and then comes to flower. Potentially, all branches may end in a flower forming a `beblätterte Rispe´ (leafy panicle) (B). The formation of strictly bracteate inflorescences may be the result either of enrichment (*En*) of the terminal flower of the main axis without (C) or with (H) reduction of the lateral shoots (*RL*) and/or of reduction of the foliage all over the shoot system (D,E: *Rfo*). *"Indem die Laubblätter im ganzen System zu Hochblattern werden, entsteht die Rispe"* (1921:72). In course of evolution the panicle may undergo diverse variations and reductions (F,G) and may finally result in a solitary terminal flower (I). In contrast to Parkin, the latter is not original but highly derived according to Pilger.

Though Pilger did not use Parkin´s term `segregation´, he clearly implied that most of the inflorescences arise from such a process. According to him it is unimportant whether the apex of the main axis remains open (B´) or terminates in a flower (B). Thus, all processes of enrichment, reduction and so on (C-G) may repeat at indeterminate shoot systems (C´-G´). Intercalary inflorescences (F´) represent nothing more than vegetative shoot systems whose lateral branches flower while the main axis remains vegetatively active. It is worth mentioning that Pilger did not require the presence of a terminal flower at all at these main axes (*"bei der man auch phylogenetisch keine Endblüte anzunehmen braucht."* 1921:77). Indeterminate bracteate inflorescences (G´) similar to those (G) which have arisen from truncation (*T*) might result after inhibition of the growth capacity of the apex (*Iap*).

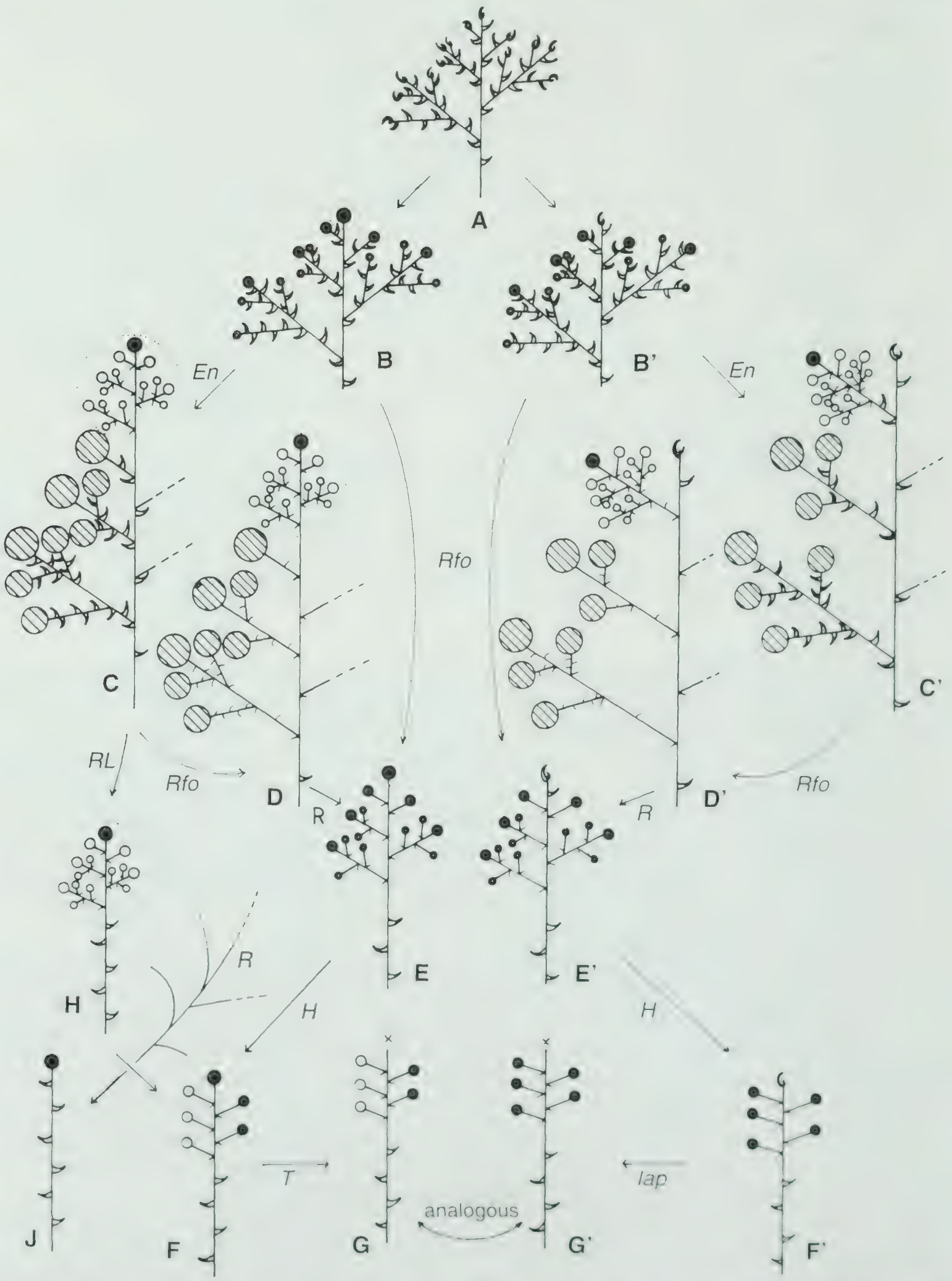


*Figure 206 - **Evolution of inflorescences after Pilger (1922)** showing the vegetative shoot system that comes to flower either at the end of all shoots (B) or at the end of lateral shoots only (B'). The leafy inflorescences evolve into bracteate inflorescences by enrichment of the terminal flowers concerned (C,C') or by reduction of the foliage all over the shoot system (E,E'). Note the analogous formation of indeterminate inflorescences by truncation of the terminal flower (G) and by inhibition of the apex (G').*

Reconstructed after Pilger 1922; compare with text.

H, homogenization, Iap, inhibition of apex, R, reduction, Rfo, reduction of foliage, RL, reduction of lateral shoot; dotted circle: terminal flowering unit relative to the entire shoot system; black: terminal flower relative to an individual leafy shoot; white: axillary flower enriching such a terminal flower

4.2.2 Wilhelm Troll and his time

Troll (1964b, 1969b) was the first to define inflorescences not in terms of their foliage, but as modified shoot systems providing flowers (*"der Blütenbildung dienende und dementsprechend modifizierte Sproßsysteme"*, 1964:5). This definition allowed him to study extended shoot systems and to recognize superior inflorescence patterns irrespective of their appearance and foliage. The result was the typological concept of inflorescences.

4.2.2.1 The typological concept of synflorescences. Troll proceeded from the premise that a compound inflorescence is composed of similar elements (fig. 207B). The terminal element plays a unique role, because it is also formed under conditions of poor nutrition when the lateral branches remain inhibited. It is termed `florescence´ (Floreszenz) or more precisely the `main florescence´ (mF) (Hauptfloreszenz). The lateral elements called paraclades (pc) repeat the branching pattern of the main axis and also bear florescences, the so-called `coflorescences´ (coF). Together the compound inflorescence is a system of florescences, a `synflorescence´ (S).

The term synflorescence was introduced by Goebel (1931:2) to characterize compound inflorescences which resemble simple ones. Troll adopted the term but restricted it to those inflorescences whose lateral branches duplicate the main axis exactly. As the main axis ends either in a terminal flower or in a non-flowering apex, only two types result: the `monotelic´ (fig. 207: A) and the `polytelic´ type (B).

- The polytelic synflorescence is composed of indeterminate florescences whose elements, individual flowers or cymes, were called `partial-florescences´ (pF). Its typical appearance is that of a disjunct indeterminate inflorescence (fig. 207B).
- The monotelic synflorescence is composed of the terminal flower (tf) and paraclades also ending in a flower (tf´, tf´´,..), thus typically corresponding to a conjunct determinate panicle (fig. 207A).

In a strict sense the latter is not composed of florescences at all, unless the individual flower is called a `monaxial florescence´ The fact that Troll nevertheless used the term `syn´florescence for monotelic systems might have had historical reasons and might be the result of similarity between the two types, each being composed of a terminal and identical lateral elements. However, by diverging from the strict meaning of the term florescence, Troll undermined his own definition of synflorescences and suffered criticism from e.g. Stauffer 1963, Zimmermann 1965, Schröder 1987, Kusnetzova 1988, Kunze 1989.

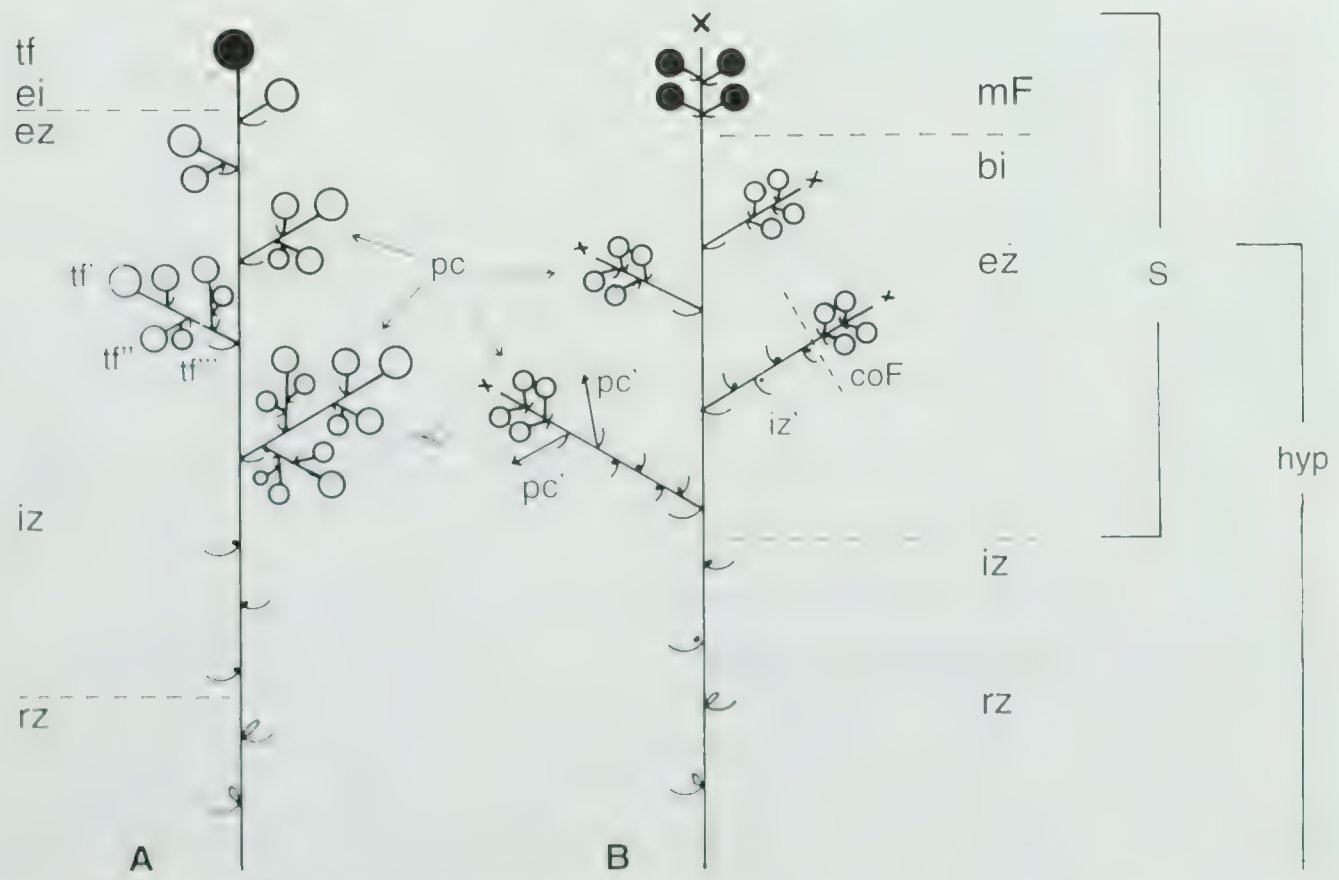


*Figure 207 - **The concept of synflorescences**. Structure and position of A, monotelic and B, polytelic synflorescences. Slightly simplified after Troll (1964) and Weberling (1981).*
bi, *basal internode*, ei, *end-internode*, ez, *enrichment zone*, hyp, *hypotagma*, iz, *inhibition zone*, mF, *main florescence*, pc, *paraclade*, S, *synflorescence*.

Troll paid particular attention to the position of the inflorescences within the plant. For this purpose he subdivided the flowering shoots into zones (fig. 207). The terminal flower in case of monotelic (A) and the main florescence in case of polytelic synflorescences (B) were separated from the enrichment zone (ez) below by a special internode, called end- (A: ei) and basal internode (B: bi). The enrichment zone bears the paraclades (pc), which terminate in a flower of 1st order (A: tf') and in a coflorescence (B: coF). The paraclades may be further branched, showing flowers and coflorescences of higher order of branches. The terminal unit, the special internode below and the enrichment zone form the synflorescence (S). An inhibition zone (iz) may be present below the enrichment zone which is followed by the renewal zone (rz) in perennial plants. Enrichment, inhibition and renewal zone form the so-called hypotagma (hyp).

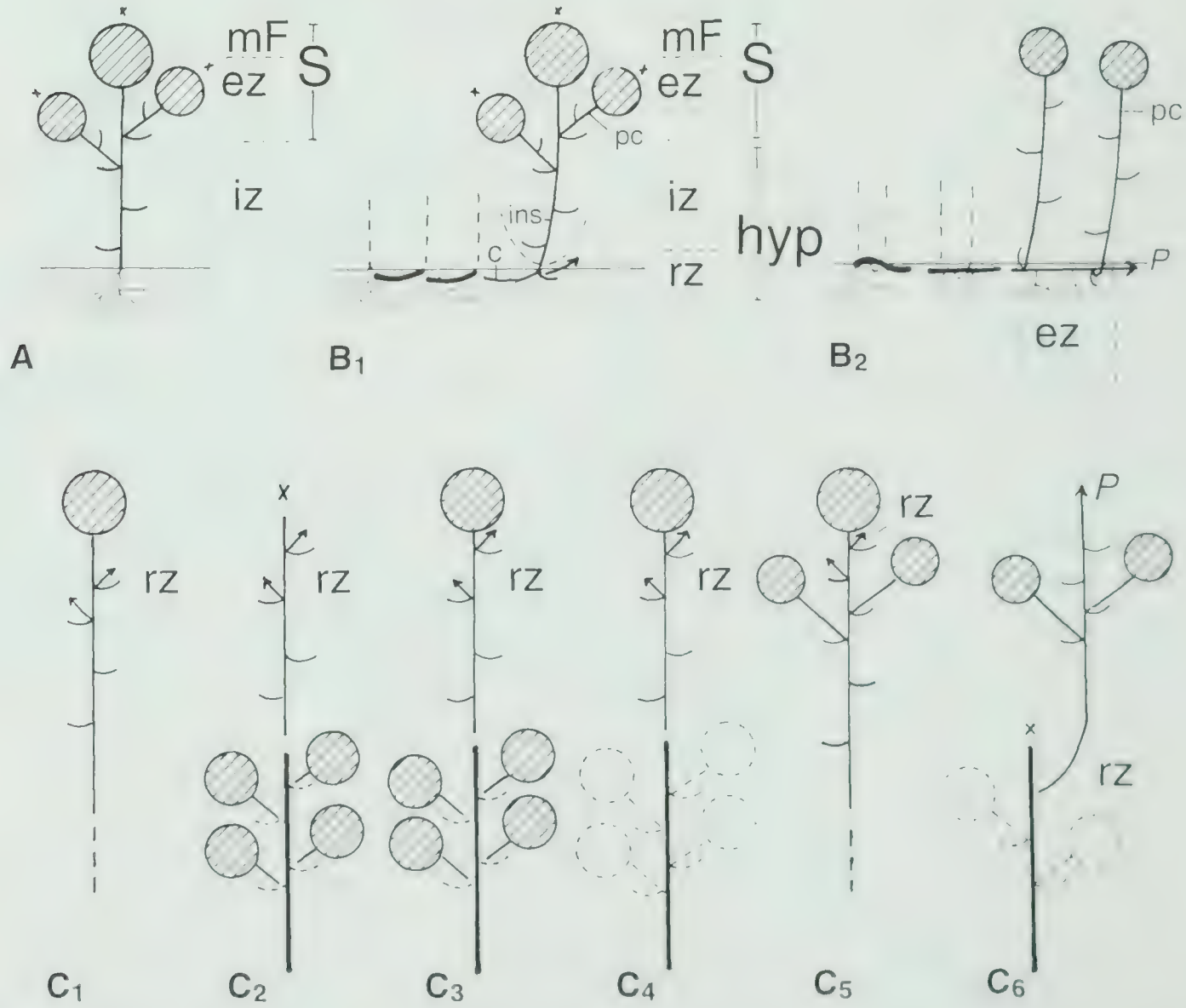


*Figure 208 - **Growth form and position of inflorescences** in annual (A) and perennial herbs (B) and in woody plants (C). Compare with text.*

c, *cryptocorm*, cz, *enrichment zone*, hyp, *hypotagma*, ins, *innovation shoot*, iz, *inhibition zone*, mF, *main florescence*, *P*, *proliferation*, pc, *paraclade*.

Troll (e.g. 1964b, 1969b) illustrated his typological concept with many examples from various angiosperm families showing the great variation in synflorescences. He paid particular attention to the process of truncation resulting in truncate synflorescences. Both monotelic (fig. 211: A_1) and polytelic (B_1) synflorescences might become truncate (A_3/B_3) by losing the terminal flower or the main florescence, leaving only the paraclades behind (T_1). As regards truncate monotelic synflorescences (A_3), these might transform into polytelic synflorescences (B_1) when their lower paraclades likewise lose their terminal flowers by truncation (T_2).

According to Troll, the open apices of polytelic and truncate synflorecences are in principle able to continue their growth, producing vegetative elements (leaves, branches) and flowers de novo (fig. 211: *P*). The fundamental process, called 'proliferation' by Troll, is thought to be always caused by a secondary return of the apex of the synflorescence to vegetative growth (e.g. Troll 1964b:77; Weberling

1982:17, Weberling & Troll 1998: 14, 49). Well known examples of the so-called `proliferating synflorescences´ are found in *Lysimachia* (Weberling 1981*Veronica* (Hamann 1958; fig. 214G,H) and in Myrtaceae (e.g. *Callistemon, Melaleuca,* fig. 218E,F; Weberling 1988a). In general, proliferation seems to occur more rarely in herbal plants, but is rather more characteristic of woody plants.

The `proliferating synflorescences´ sensu Troll largely correspond to the `intercalary inflorescences´ sensu Parkin. But in contrast to his predecessors, Troll considered them to be advanced structures, resulting from determinate inflorescences by truncation and proliferation.

As regards the formation of inflorescences in plants of different life forms, Troll referred the term synflorescence to the entire flowering shoot system of one season (fig. 208):

- The annual herb (A) lacks any renewal shoots. The whole plant flowers, produces seeds and then dies off. For that reason the whole plant corresponds to a synflorescence and a more or less extended inhibition zone.
- The perennial herb (B) is characterized by renewal buds which usually appear at the base of the overground shoot system near the ground level (B_1: rz). After flowering and fruiting the overground part of the plant dies off while the subterranean part survives and renews the overground shoot system in the next season. Troll (1964:282) called the latter `cryptocorm´ (c) and the renewal shoots `innovation shoots´ (ins) (`Innovationstriebe´, `Erneuerungstriebe´). He compared the entire annual shoot system of the annual herb (A) with each of the annual innovation shoots of the perennial herb (B_1) which are only distinguished from the first in having renewal zones at their bases.

  This comparison is very evident, but holds true for sympodial cryptocorms only (B_1) where the inflorescence terminates the main axis and thus corresponds to an entire synflorescence. However, in monopodial cryptocorms (B_2), e.g. *Paris quadrifolia* (Troll 1937:708), the inflorescences are arranged laterally on a prostrate shoot whose apex remains active for several seasons (*P*). The individual overground shoot system bearing a terminal inflorescence does not correspond to an entire innovation shoot but only to a flowering lateral shoot which has no renewal capacity at all. Consequently it has to be called a paraclade (pc) of a proliferating synflorescence. As the two overground shoot systems in B_1 and B_2 have different positions within their plants, they are not comparable to each other.
- Troll not only compared the flowering shoot system of an annual plant (A) with the flowering innovation shoot of a perennial herb (B_1) but also the latter with the flowering innovation shoot of a woody plant (C). However, as woody plants are characterized by extended and persistent overground vegetative shoot systems, Troll had to distinguish different ways for the formation of inflorescences. Focussing on woody plants of temperate climates he postulated: *"Entweder gelangt der jeweilige Endtrieb zur Blüte oder aber es erfolgt die Blütenbildung an seitlichen, gewöhnlich dem vorjährigen Langtrieb entstammenden Kurztrieben"* (1962:92). As regards the first case (C_1), the flowering innovation shoot is directly comparable to that of a sympodial perennial herb (B_1) as the terminal synflorescence is separated from the persistent part of the shoot system by a hypotagma including the renewal zone. As regards the second case (C_2), each of the flowering shoot systems either corresponds to an annual plant (A) or as far as they have a renewal zone of their own, to an innovation shoot of a sympodial perennial herb (B_1). Ignoring the different ways of renewal, even the combination of both possibilities (C_3), is compatible with the concept of synflorescences.

  However, if one considers sylleptically branched flowering shoot systems, the application of the concept again becomes unsatisfactory (C_4-C_6). The individual innovation shoots may be different and thus result in different synflorescences within a single shoot system (C_4, e.g. *Nebelia laevis, N. paleacea, Raspalia variabilis*, fig. 111B, 115, 151). But more important is the fact that the zonation of the innovation shoot is changed. In regular sympodial shoot systems (C_5: e.g. *Lonchostoma monogynum, Raspalia staavioides, Staavia glutionosa*, fig. 85D,E, 137, 166A) the renewal zone may appear among the flowering branches. In those being characterised by monopodial inserts (C_6 e.g. *Audouinia capitata, Berzelia arachnoidea, Linconia alopecuroides*, fig. 8A,C, 30, 79D) renewal shoots may either appear above the flowers (rz) or lack completely being substituted by the apex (*P*) which grows on as in the monopodial perennial herbs (B_2). By including persistent vegetative parts of the shoot system in the unit of the synflorescence, Troll abandoned his own

definition of a synflorescence (see p. 244) and the common agreement that inflorescences are caducous (usually annual) shoot systems.

4.2.2.2 The dynamic concept of cyclic evolution. Troll was a typologist and interested in the diversity of inflorescences. He of course noticed the possible transformation of a monotelic into a polytelic synflorescence, but never interpreted it in a phylogenetic sense. In contrast to him, Maresquelle (1970) and Sell (1969, 1976) formulated evolutionary tendencies and thus extended Troll's ideas. As a result of their detailed studies on the phenology of flowering in compound inflorescences, they were able to show that all inflorescences might be derivable from each other by a few reiterating elementary processes:

As fig. 209 illustrates, a terminal flower merges into an inflorescence by being enriched (*En*) with axillary flowers in a basipetalous direction (arrows). A tendency is present in these inflorescences to reverse the flowering sequence into an acropetal one ('razemization', *Rz*), thus following the mode of initiation of the flowers. In doing so the apex may be completely consumed by producing axillary flowers and not able to form a terminal flower any more ('truncation', *T*). The result is an upward flowering indeterminate inflorescence which again may pass through the processes of enrichment, razemisation and truncation. Maresquelle (1970) explained his ideas by presenting examples from Brassicaceae, Fabaceae and Asteraceae and finally came to the conclusion that the scheme given in fig. 209 may be generalized, substituting the terminal flower by any terminal inflorescence.

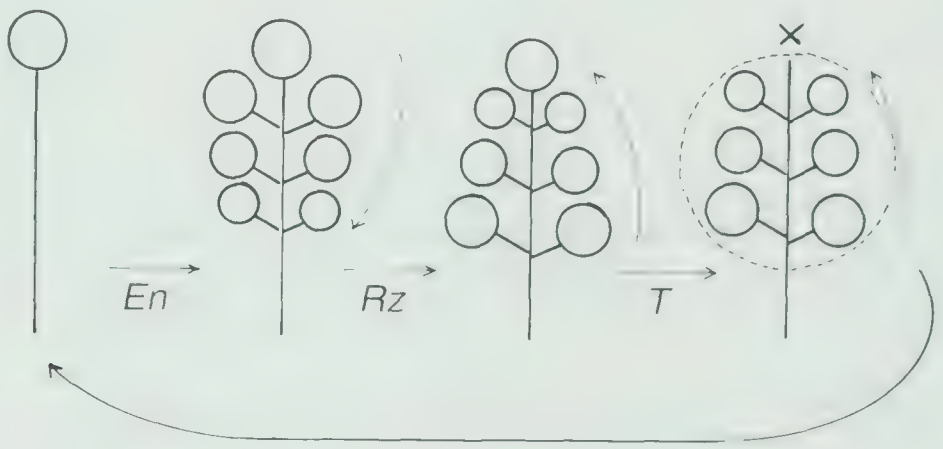


*Figure 209 - **The concept of Maresquelle (1970)** showing the cyclic reiteration of the transformation of any terminal unit into an indeterminate upward flowering unit by the elementary processes of enrichment, razemization and truncation. Rz, razemization.*

Sell (1969, 1976) completed the concept of Maresquelle. Studying the inflorescences of numerous angiosperm families, he was able to recognize the same pattern: A downward flowering panicle-like structure bearing flowers or any kind of inflorescences is subjected to razemization, resulting in an acropetally flowering upper part and a still basipetalous flowering lower part (fig. 210 *Rz*). Sell found razemization always to be accompanied by 'homogenization' (*H*), a process that leads to increasing uniformity of the lateral shoots in the terminal as well as in the lateral units. After truncation (*T*) a disjunct inflorescence results, being composed of several upward flowering racemes. Sell generalized that racemes always arise from panicles by razemization, homogenization and truncation (e.g. Rosaceae, Rutaceae) and that double racemes or even more compound inflorescences may have arisen from racemes by gradual enrichment (e.g. Acanthaceae, Fabaceae, Brassicaceae, Lamiaceae, Asteraceae). Further evolutionary tendencies like 'capitularisation' and 'synchronisation' which are best developed in Asteraceae, result in flower-like inflorescences which may repeat the evolution of inflorescences on a higher level of complexity (compare with Claßen 1984, Claßen-Bockhoff 1992, 1996).

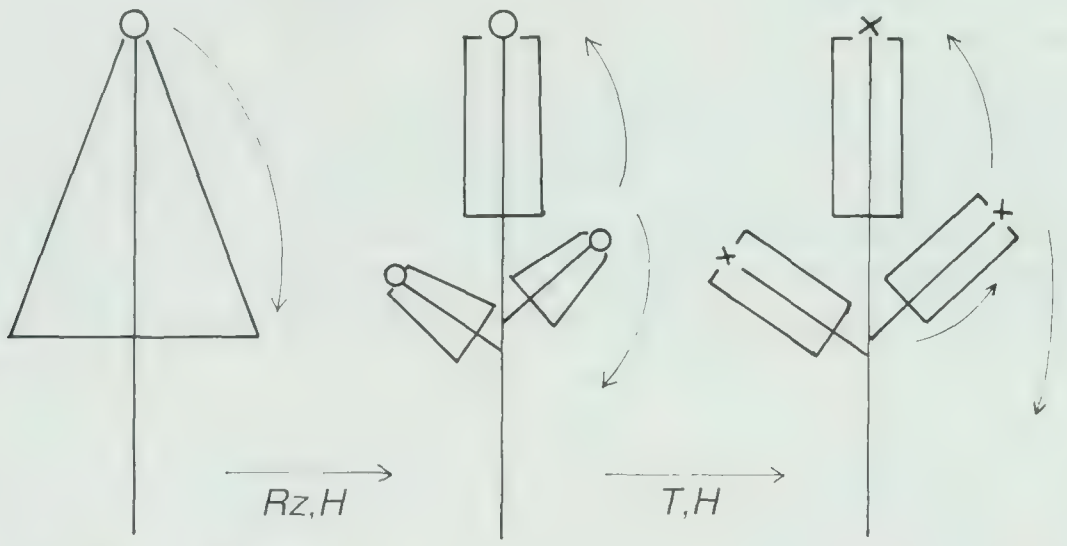


*Figure 210 - **The concept of Sell (1976)** showing the transformation of a determinate downward flowering panicle into a disjunct inflorescence composed of racemes, by the elementary processes of razemization, homogenization and truncation. Note that the elements of the panicle and the racemes may be flowers or inflorescences of any kind.*
Rz, razemization.

The concepts of Maresquelle and Sell are based on physiological considerations. Applying to the generally accepted concept that an antagonism between a basipetal effect coming from the apex and an acropetal effect coming from the base exists along the main shoot of a plant, the extension of the terminal inflorescence depends directly on the vegetative vigour of the main shoot. The downward enrichment of the terminal flowering unit "*results from a step-by step cancellation of the basipetalous inhibitory effects...*" (Sell 1980:286). The resultant lateral flowering units are taken as `réalisations renouvelées d'une même décision' that is as `morphogenetic repetitions' of the terminal unit (Maresquelle & Sell 1965: 98). The gradient is set up by long-range interactions which are considered to be fundamental, while razemization may result from short-range interactions being evolutionary advanced. Following Sell it is thus fully acceptable that the downward flowering panicles represent a more primitive stage than the upward flowering racemes. He furthermore found a confirmation for this evolutionary tendency in the growth form of the plants, as woody plants tend to have determinate and herbs predominantly indeterminate inflorescences.

The evolutionary tendencies introduced by Maresquelle and Sell were incorporated into the Trollian concept without delay (see Weberling 1983a,b). The combination of both, the typological and the evolutionary concept, is illustrated in fig. 211:

Monotelic synflorescences (A_1) may change into polytelic (B_1) synflorescences by means of the three elementary processes truncation (*T*), homogenization (*H*) and razemization (*Rz*). Depending on their sequence transitional forms result: monotelic truncate synflorescences (A_3) and monotelic disjunct synflorescences (A_2). The latter are characterized by florescence-like elements which are, however, composed of the terminal flower and the uppermost paraclades of the enrichment zone. For this reason Troll called them `pseudo-florescences' (psF). In fact they are only `pseudo'-structures following his type definition; relative to the physiology of morphogenetic repetitions they appear to be natural units.

In the same manner as monotelic synflorescences change into truncate ones ($A_1 \rightarrow A_3$) by loss of the terminal flower of the main axis (T_1), polytelic synflorescences become truncate in a superior way ($B_1 \rightarrow B_3$) by loss of the main florescence (T_3). The result are polytelic synflorescences of 2^{nd} order. Theoretically the evolutionary processes may repeat several times each time resulting in another more compound polytelic synflorescence (T_n). The open apices of the monotelic truncate (A_3), polytelic (B_1) and polytelic truncate (B_3) synflorescences may secondarily return to vegetative growth by proliferation (*P*) resulting in various forms of `proliferating synflorescences' (A_4, B_2, B_4).

The studies of Maresquelle (1970) and Sell (1969, 1976, 1980)
(1) released the Trollian concept from its strict typological nature by considering physiological aspects,
(2) demonstrated the dynamics of inflorescence change in the course of evolution,

(3) proved that there are good reasons for accepting monotelic synflorescences as less advanced than polytelic synflorescences and
(4) showed that florescences may arise by two different evolutionary pathways, by enrichment of a terminal unit (fig. 209) and by its subdivision (fig. 210).

However, Maresquelle inexplicably did not number the process of enrichment among the elementary steps and this aspect has hitherto been largely neglected until now, not being included in the concept of synflorescences. As a result solitary flowers are always interpreted as being derived structures though the concept of Maresquelle principally allows as well for them interpretation as primitive.

*Figure 211 - **General scheme illustrating the evolution of synflorescences** by including the ideas of Maresquelle and Sell into the Trollian concept. A_1, monotelic conjunct, A_2, monotelic disjunct, A_3, monotelic truncate, A_4, monotelic proliferating, B_1, polytelic, B_2, polytelic with proliferating florescence, B_3, polytelic truncate, B_4, polytelic with proliferating enrichment zone. Note that there are more transitional forms between the monotelic and the polytelic type as shown here because the processes concerned are independent from each other. Curved arrows: flowering sequence.*
ez, *enrichment zone*, mF, *main florescence*, P, *proliferation*, psF, *pseudo-florescence*, Rz, *razemization*.

4.2.3 Current views of inflorescence morphology

At present about 20.000 species from numerous angiosperm families have been investigated, using the concept of synflorescences (Weberling 1983b, for references see Weberling 1989). Most of the papers were written in German, but Weberling (1965, 1982, 1983b, 1989) repeatedly tried to introduce the concept into the English speaking world. He summarized the evolutionary tendencies and stressed the necessity of recognizing identical structural elements within flowering shoot systems as the base for homology and thus for the systematic value of inflorescence morphology (1963, 1971, 1983a). However both the question of homology and the systematic value of synflorescences with respect to woody plants, have been widely debated.

4.2.3.1 Typology, terminology and the question of homology. Troll realized that the manifold inflorescences agree in having a terminal flowering unit and a more or less extended enrichment zone, with lateral shoots bearing identical flowering units. Drawing attention to this conformity he introduced the term synflorescence. Historically, he applied the term first to polytelic and then to monotelic synflorescences. Troll's typological method and restrictive definition of the term synflorescence were

criticized from the outset, but the concept of evolutionary repetition provoked new objections to Troll's concept (Kusnetzova 1988, Kunze 1989).

Kunze (1989) pointed out that repetition of the evolutionary processes at different levels of organization results in a hierarchy of types e.g. monotely, polytely of 1st, of 2nd, of 3rd order and so on (fig. 211:T_n). As each level is reached by the same processes, the polytelic type sensu Troll in fact covers several types, each being as different from the others as is the monotelic from the polytelic type sensu Troll. Kunze concluded that the formation of only two types was an unacceptable restriction in that it ignored evolutionary repetition.

The hierarchy of types raises questions about the real nature of a synflorescence. Is it a type which allows identification of homologous elements or is it a pattern which is repeated at different levels of evolution, thus producing analogous forms, or is it both? The manner in which Troll compared the terminal units of the two types of synflorescences (flower/main florescence) and contrasted them with paraclades (fig. 207) did not clearly show whether he held synflorescences to be homologous or analogous structures (see Schröder 1987: 457, Kunze 1989:193).

As regards homology, it is possible to identify homologous elements only within each of the types (compare with fig. 207). The terminal flower is homologous to the uniflorous paraclades in a monotelic synflorescence (A_1) and the main florescence is homologous to the coflorescences in a polytelic synflorescence (B_1). Relative to this context Troll (1964: 149) emphasized that partial florescences (pF) are fundamental different from paraclades (pc), and this is in fact the case within the individual polytelic synflorescence. But it cannot be said that paraclades of a monotelic and a polytelic synflorescence are homologous units. The concept of evolutionary repetition clearly shows that the terminal units are analogous. Paraclades of a monotelic synflorescence likewise merge into partial florescences and paraclades of a polytelic synflorescence after being transformed by means of razemization, homogenization and truncation (fig. 211). Thus, partial florescences and paraclades are not fundamentally different, but represent two different levels of evolutionary transformation (Kunze 1989: 194). Once the similar subdivision of different types is taken into consideration, the level of comparison changes from homology to analogy. As a consequence, it is not advisable to compare the monotelic and polytelic types from the standpoint of homology because the types represent two extreme forms of a continuous series and have evolved on different pathways. From the standpoint of analogy, however, the comparison of the types may be very interesting, because their similar positional subdivision points to a similar gene expression and regulation relative to reproductive units.

Synflorescences appear to represent both, types capable of use as a base for homology relative to a certain evolutionary level, and patterns being repeated on different levels of organization. Accepting this, a strict distinction between monotelic and polytelic types appears unnecessary, as the polytelic synflorescences merely repeat the pattern of the monotelic ones. A synflorescence then may be defined as *"...an aggregate of flower-bearing axes including a principal axis capped by floral units of any nature and paracladia bearing floral units of the same nature"* (Kusnetzova 1988: 4). In doing so, the analogy aspect comes to the fore rendering the terms 'florescence' and 'pseudoflorescence' unnecessary. This is acceptable, because the evolutionary concept has shown that, besides truncation, further developmental processes are involved into the course of evolution: flowering sequence, disjunction and enrichment play an equally important role to that of truncation. Moreover, the repetition of synflorescence-like patterns on higher levels of organization clearly indicates that the importance of the main axis is only relative to other axes.

As a summary, fig. 212 shows a general scheme depicting the dynamic concept of inflorescence evolution. Special attention is given to the process of enrichment which in fact permits evolutionary repetition (see Maresquelle 1970, Sell 1976) and to the process of reduction which allows secondary simplifications and thus return to a lower level of organization which in turn permits and indeed forces new evolutionary pathways (compare with Claßen 1984, Claßen-Bockhoff 1996).

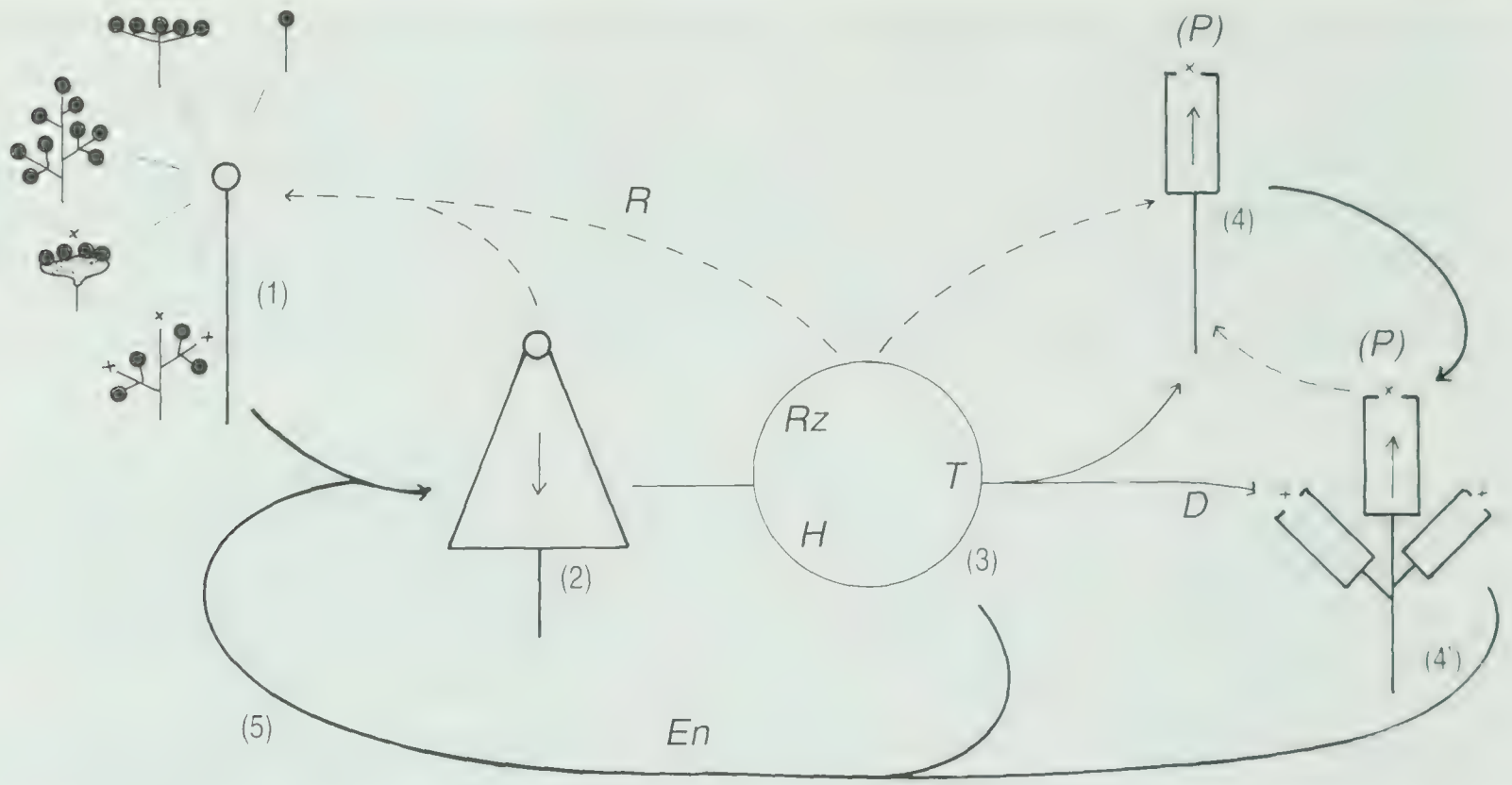


Figure 212 - ***General scheme depicting the dynamic concept of inflorescence evolution.*** *Starting with any floral unit (1) the process of enrichment results in a downward flowering panicle-like structure (2). After the formation of various transitional forms (3) by razemization, homogenization and truncation (circle) a simple (4) or disjunct synflorescence (4') appears, which is able to repeat the same processes being enriched first (5) and then transformed into a disjunct synflorescence of a higher level of organization. Note that this tendency towards greater complexity is opposed by the process of reduction which resimplifies inflorescences and thus opens new evolutionary pathways.*

D, disjunction, P, proliferation, R, reduction, Rz, razemization; dotted line: reduction; thick line: enrichment; thin line: transition from monotely/polytely to polytely of any order.

4.2.3.2 Inflorescences, synflorescences and flowering shoot systems in woody plants. The application of Troll's concept to woody plants, particularly of the tropics, posed many problems *"Difficulties may derive from prolepsis and syllepsis of the innovation shoots, prolification of the inflorescence axis and, abundantly, by the deficiency of clearly marked limits between sprouts growing in different seasons."* (Weberling 1983b:917). But several more questions arise concerning the nature of florescences and paraclades (Jäger 1980, Bayer 1994), the lifespan (Endress 1970, Jager 1980) and delimitation (Van Steenis 1963, Schröder 1987) of a synflorescence and the phylogenetic interpretation of synflorescences in woody plants (Briggs & Johnson 1979), all resulting in one fundamental question: what does a synflorescence sensu Troll represent, a caducous inflorescence or a flowering shoot system including perennial elements?

Troll studied the structure of inflorescences and certainly accepted the view of an inflorescence as a caducous flowering shoot system. He recognized that all inflorescences were in fact 'syn'florescences and on this basis introduced his typology. Troll also studied the position of these inflorescences within the plant bodies of annual and perennial plants, referring either to the whole annual plant or to the seasonal innovation shoot (fig. 207, 213A). He recognized that these flowering shoot systems are subdivided into a terminal synflorescence (S) comprising the shoot tip and the enrichment zone, and a vegetative part below, including the inhibition zone (iz) and the renewal zone (rz). Though Troll's definition of a synflorescence as 'a system of florescences' lacked any delimitation, the latter was implied by the zonation of the flowering shoot system that separated synflorescences from the inhibition and renewal zones below and thus preserved their caducous nature.

Until now it has been largely overlooked that Troll actually studied two different levels of complexity caducous inflorescences and perennial shoot systems bearing inflorescences. In annual plants (fig. 208A) both levels coincide, as the entire plant dies off after seed set. The entire plant corresponds to a

single inflorescence. It does of course bear vegetative parts so that the plant can strengthen its shoot system, assimilate, defend against heat, frost, browsing and so on, but all these vegetative structures are ephemeral and exist only to guarantee the realization of the superior function: to produce pollen and seeds. But in woody plants inflorescences and flowering innovation shoots represent two different units and must be treated as separate (fig. 213B,B′). To distinguish the two levels, to both of which Troll applied the term `synflorescence′, the terms `synflorescence s.str.′ (= caducous inflorescence) and `synflorescence s.l.′ (shoot system bearing inflorescences) are used in the following paragraph.

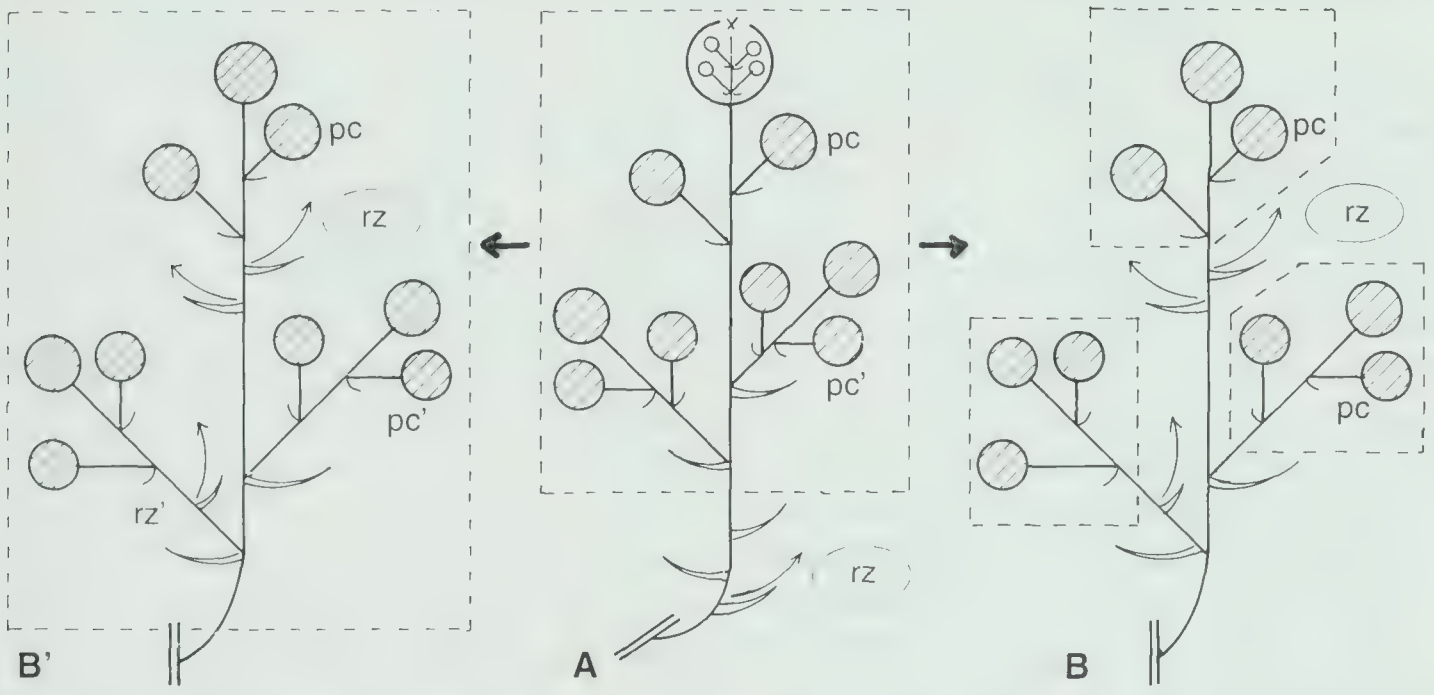


Figure 213 - ***Inflorescences, synflorescences and seasonal shoot systems****. A, profile of a flowering innovation shoot of a perennial herb showing the terminal caducous inflorescence (= synflorescence) and the renewal zone below, B,B′, profiles of flowering innovation shoots of a woody plant illustrating the two levels of organization: the caducous inflorescence (B: dotted lines) and the persistent shoot system bearing inflorescences (B′: dotted line). Note that the term synflorescence is ambiguous. It is referred to the caducous inflorescence above the renewal zone in A and B (synflorescence s.str.) and to all flowers of an innovation shoot in A and B′ (synflorescence s.l.). Troll used the second definition (B′), dealing with flowering shoot systems rather than with inflorescences.*

pc, *paraclade,* S, *synflorescenc; dotted line: delimitation of a synflorescence sensu Troll referring the term either to all flowers of an innovation shoot (A,B′) or to each of the individual flowering units above and below the renewal zones (A,B).*

Troll himself either did not realize or ignored the fact that he changed his reference system. As with perennial herbs (A), Troll applied the term synflorescence to the entire flowering innovation shoot of woody plants (B′) ignoring the distal position of the renewal zones in overground shoot systems and thus accepting the appearance of persistent shoots within a synflorescence. He did not consider the fact that the resulting synflorescence no longer corresponded to an inflorescence, but to a persistent shoot system bearing renewal shoots and terminal and/or lateral inflorescences. One reason for this might have been that in temperate climatic zones the clearly recognizable growth cycles offer well delimited units for comparison. A second reason might have been that the arrangement of individual inflorescences within a woody shoot system resembles the arrangement of individual florescences within a caducous synflorescence (see fig. 213). But nevertheless it is astonishing that neither Troll nor his followers took into consideration the fact that a synflorescence might be delimited by the renewal zone below, that the resultant similar patterns thus would be analogous in nature and that the supposed paraclades would represent individual synflorescences (B) instead of elements of a single superior synflorescence (B′).

The main consequence of applying the term synflorescence to woody shoot systems sensu Troll was the resulting homology with caducous inflorescences and the careless transfer of evolutionary tendencies from annual herbs to woody plants. As determinate synflorescences were thought to be more primitive than indeterminate synflorescences (fig. 211, 212) it was assumed that open apices in woody shoot systems represented a derived condition. All innovation shoots bearing only lateral inflorescences were interpreted to have truncate synflorescences (fig. 208 C_6) and all of them continuing in a monopodial

manner were thought to represent proliferating synflorescences (fig. 208:C_4) (e.g. Troll 1964-1972, Rauh 1975, Jäger 1980, Jahnke 1984, Weberling 1985, 1992, Weberling & Herkommer 1989, Tissot & Weberling 1993, Bayer 1994, Weberling & Troll 1998). As proliferation sensu Troll always meant a secondary reactivation of a formerly flowering apex (Weberling 1982:17), the result was an innumerable amount of highly derived synflorescences in woody plants. This is incompatible with the generally accepted view that woody plants, particularly those of the tropics, represent a rather primitive group amongst higher plants (see p. 288). It is also incompatible with the occurrence of highly derived synflorescences in so-called 'primitive' Angiosperms (Weberling 1988b, 1992).

The application of the term synflorescence to woody plants sensu Troll required a number of concessions. Some examples were selected to illustrate the problems and the diverse interpretations of individual authors:

- Hamann (1958, 1960) studied inflorescences in *Veronica* and its shrubby New Zealand counterpart *Hebe* (fig. 214). He was influenced by Troll's early comments on inflorescence morphology, but, having regard to the similar subdivision of acrobotrytic (with terminal raceme: E) and pleurobotrytic species (with terminal cluster of lateral racemes: F), he argued that the term 'synflorescence' might become a term for analogous forms. He thus drew attention to the problems relating to pseudoflorescences and pattern repetition at different levels of complexity (see § 4.2.3.1).

  Studying the inflorescences of the genus *Veronica* first, Hamann (1958) concluded that the acrobotrytic species (E) represented the more primitive and the pleurobotrytic species (F) the more advanced stage of inflorescence evolution. His main argument was that he found the lateral racemes in both groups to be homologous. He was able to show that the perennial species renew predominantly from below the inflorescences. Only in some species 'proliferating' inflorescences appeared resulting from both, terminal racemes (only *V. filiformis:* G) and terminal clusters of lateral racemes (e.g. *V. officinalis:* H). In accordance with Troll's concept, he interpreted these forms as being derived and attempted to explain the appearance of proliferation regarding to the biology of the plants concerned (see also Thaler 1951, Kaussmann 1954, Weberling & Troll 1998): *V. filiformis* is an invader from the Causcasus Mountains. The combination of a vegetatively active main shoot and stem-borne adventitious roots allows the plant to become perennial and to propagate by individualization of isolated shoot sections. The orthotropic flowering shoots in *V. officinalis* return to plagiotropic growth after fruit set, producing adventitious roots and thus providing the option of dormancy. Those shoots which nevertheless die off during winter lead over to the shoots of other pleurobotrytic species which always produce some apical leaves before the apex dies off.

  Continuing his studies in *Hebe*, Hamann (1960) found most species to be similar to the pleurobotrytic *Veronica* species. He first thought (Hamann 1958) that these forms would be more derived than the acrobotrytic *Veronica* species (E), but after having analysed *H. diosmifolia* in more detail he changed his mind. The shoots of this species are highly variable (A-D). Hamann (1960) concluded that the number of lateral racemes increased with decreasing vegetative vigour and that the flowering impulse finally extended even to the main shoot, resulting in a terminal raceme. He hypothesized that in *Hebe* the 'paniculate' inflorescence (D) proved to be more advanced than the pleurobotrytic inflorescence (A-C) - the reverse of the situation in *Veronica*.

  Hamann (1958, 1960), though influenced by Troll, demonstrated an independence in interpreting his findings. He tried to correlate the position of inflorescences with the vegetative vigour of the shoot system (in *Hebe*) and with the growth form of the plant (in *Veronica*), both of which aspects refer to the architecture of the plant (see § 4.2.4). He differed from Troll in taking the 'proliferating synflorescences' in *Hebe* to be primitive, in supposing a terminalization relative to the flowering impulse and in accepting different modes of inflorescence formation in woody and herbaceous plants

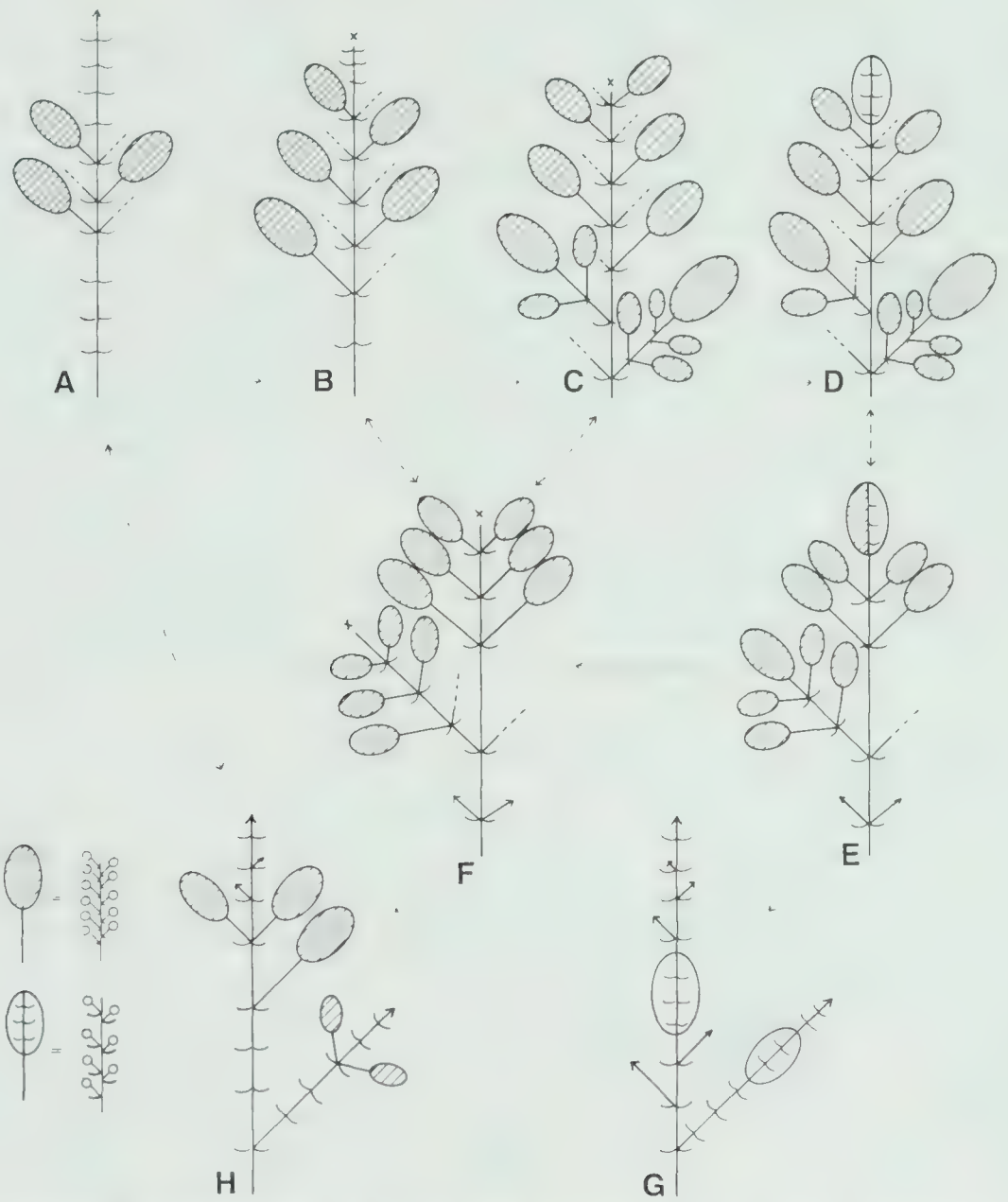


Figure 214 - ***Flowering shoot systems in* Hebe *and* Veronica**. *A-D,* Hebe diosmifolia *showing the high variability of flowering shoots within an individual plant, E,* Veronica persica, *representing the acrobotrytic group, F,* V. latifolia, *representing the pleurobotrytic group, G,* V. filiformis *and H,* V. officinalis, *both species with protruding main shoots. Note that 'proliferation' is thought to be primitive in the woody* Hebe *(A) and derived in the herbal* Veronica *(G,H) arrows: direction of derivation; dotted lines: similarities between presumed primitive and advanced inflorescences in* Hebe *and* Veronica. *After Hamann (1958, 1960), changed and simplified.*

- Endress (1970) studied the flowering shoot systems of apetalous Hamamelidaceae and contrasted the innovation shoot of *Distylium* sp. (fig. 215: B) with the two season old shoot system of *Parrotia* sp. (A) If following Trollian concepts, he would have been obliged to compare the innovation shoot of *Distylium* (B), representing a botryoid synflorescence, with the flowering shoots of only the most recent season of *Parrotia* (A: n), each representing a botrytic florescence (dotted line). Endress considered these units too different to be directly comparable, but drew attention to several points of correspondence between the innovation shoot of *Distylium* and the two season old shoot system of *Parrotia* (thick lines) However these points of correspondence refer to flowering shoot systems and not to inflorescences. The analogous pattern is nothing more than the expression of a similar arrangement of flowering units within a shoot system, whereby the resting period in *Parrotia* may represent a variation in time possibly induced by long-time climatic conditions. Comparing the next level of organization, that is the caducous inflorescences (black), the level of correspondence would be maintained. Relative to this reference system *Distylium* has uniflorous inflorescences and *Parrotia* racemes This interpretation also corresponds to Endress' study and illustrates that the separation of the two aspects, persistent flowering shoot system and caducous inflorescences, may bring clarity to the interpretation of inflorescence morphology.

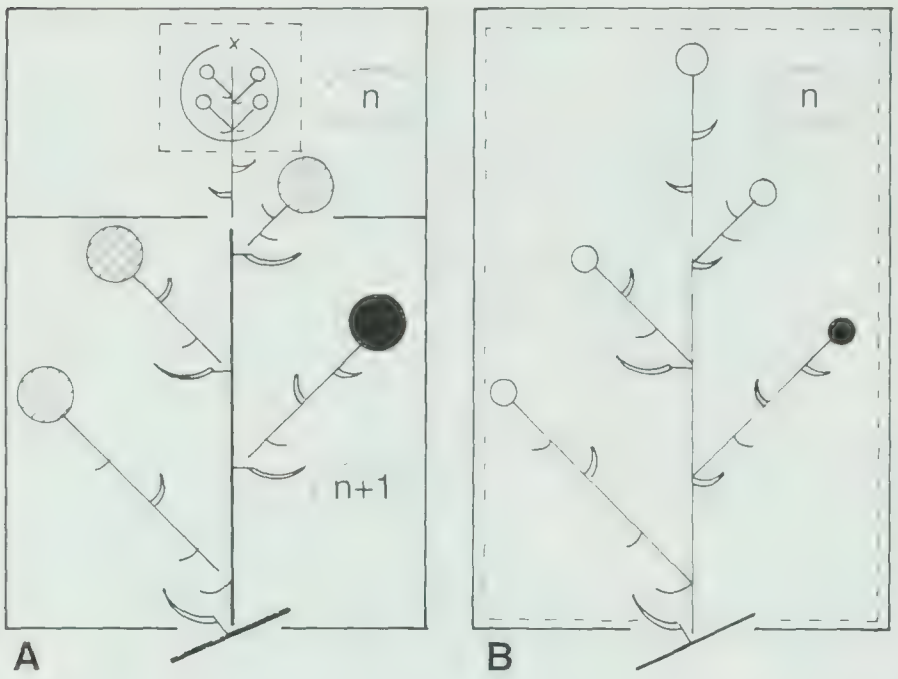


*Figure 215 - **Flowering shoot systems of selected Hamamelidaceae**. A, profile of a two season old shoot system of* Parrotia, *B, profile of an innovation shoot of* Distylium *with renewal buds between the individual flowers (not shown). Following Troll, the flowering shoot systems of season n are comparable units (dotted line). Endress (1970) however preferred to compare the two entire shoot systems (thick line) regardless of their different ages. He thus compared flowering shoot systems rather than inflorescences. Defining inflorescences as caducous flowering units,* Distylium *has uniflorous and* Parrotia *racemous inflorescences (black). After Endress 1970, redrawn and slightly changed.*

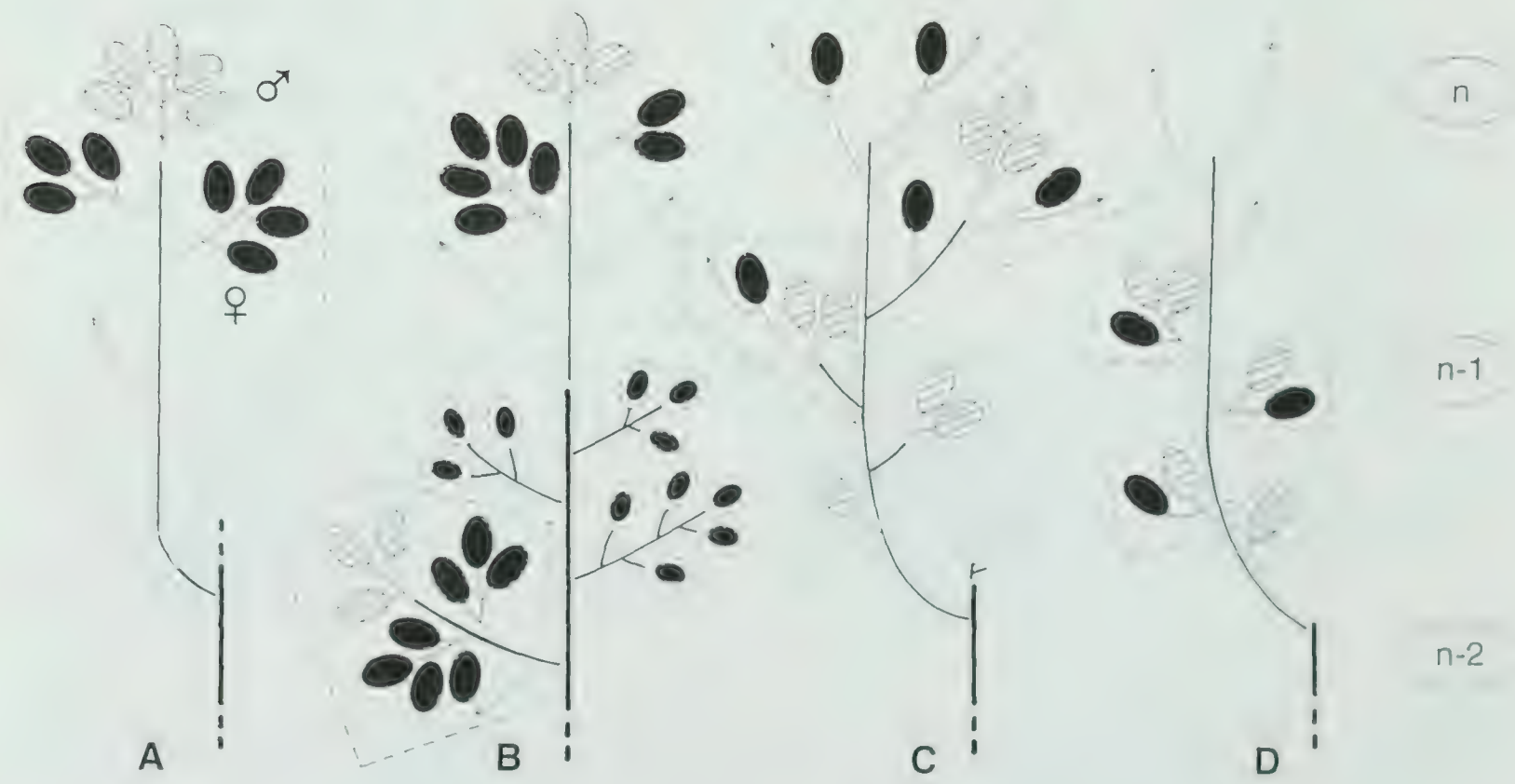


*Figure 216 - **Flowering shoot systems of selected Betulaceae**. Profiles of A,* Alnus glutinosa, *B,* A. viridis, *C,* Corylus avellana, *D,* Betula nana *illustrating the diverse arrangement of male (hatched) and female (black) catkins within the family. The dotted lines indicate the units which represent paraclades following Jäger (1980). Note that e.g. in A the whole flowering canopy might be a single synflorescence and also that the catkins become dormant so that the formation of renewal shoots varies in time among the species. This renders more difficult the delimitation of the innovation shoot which represents the reference system in Troll's concept. After Jäger 1980, redrawn and slightly changed.*

■ Jager (1980) addressed similar questions in a study of the Betulaceae. He was confronted with a pattern composed of male and female catkins (fig. 216 A) that recurred within the family, but was largely masked by shifts in time and position relative to the renewal zone. Though some of these patterns resemble synflorescences sensu Troll, Jager did not regard them as such because the lateral female catkins differed from the terminal males in sex and structure and thus did not correspond to the definition of paraclades. Jäger (1980:93) restricted the term paraclade to those lateral shoots

which bear clusters of both male and female inflorescences and thus repeat the entire terminal unit. In doing so he accepted the perennial nature of a synflorescence. He interpreted solitary male catkins (C,D) as reduced paraclades and solitary female catkins as the base of a truncate (C) or proliferating (B) synflorescence (Jäger 1980: 98). He furthermore found `monopodial´ (B) and `sympodial proliferations´ (D) and renewal shoots below (B) and above (D) the flowering shoots as well as on female branches (C).

Like Endress (1970) before him, Jäger (1980) in fact studied the highly diverse arrangement of the catkins within the family, an aspect which is more related to the architecture of woody plants (see § 4.2.4) than to inflorescence morphology. He applied the term synflorescence to extended flowering shoot systems and did not associate it with an individual innovation shoot. Had he done so, he would have had to deal with issues such as the production at the end of season n-1 of catkins which remain dormant (either naked or as enclosed buds) before coming to flower at the beginning of season n. A further point requiring explanation is the fact that the renewal shoots either sprout in the middle of season n (C), or do so kataleptically (A,B,D). Similar chronological variability is quite common and not restricted to Betulaceae (see § 4.2.4). This highlights the inadequacy of the innovation shoot as a reference system in the study of synflorescences sensu Troll.

- Bayer (1994) studied the inflorescences of Malvales and found a specialized type of inflorescence called `Bicolor-Endverzweigung´ (fig. 217B) to be rather common within the taxa studied. This kind of inflorescence (which does not follow the definition of a florescence sensu Troll) appears in a terminal and/or lateral position and may be reduced relative to the number of flowers and/or leaves. In the extreme case only one axillary flower appears (C). Following Troll, Bayer (1994) referred the term synflorescence to the entire innovation shoot, accepting the appearance of woody shoots within the synflorescence. He concluded that a monotelic synflorescence determined by a terminal Bicolor-Endverzweigung (A) represented the primitive and a spike-like polytelic synflorescence the most advanced condition within the family (C).

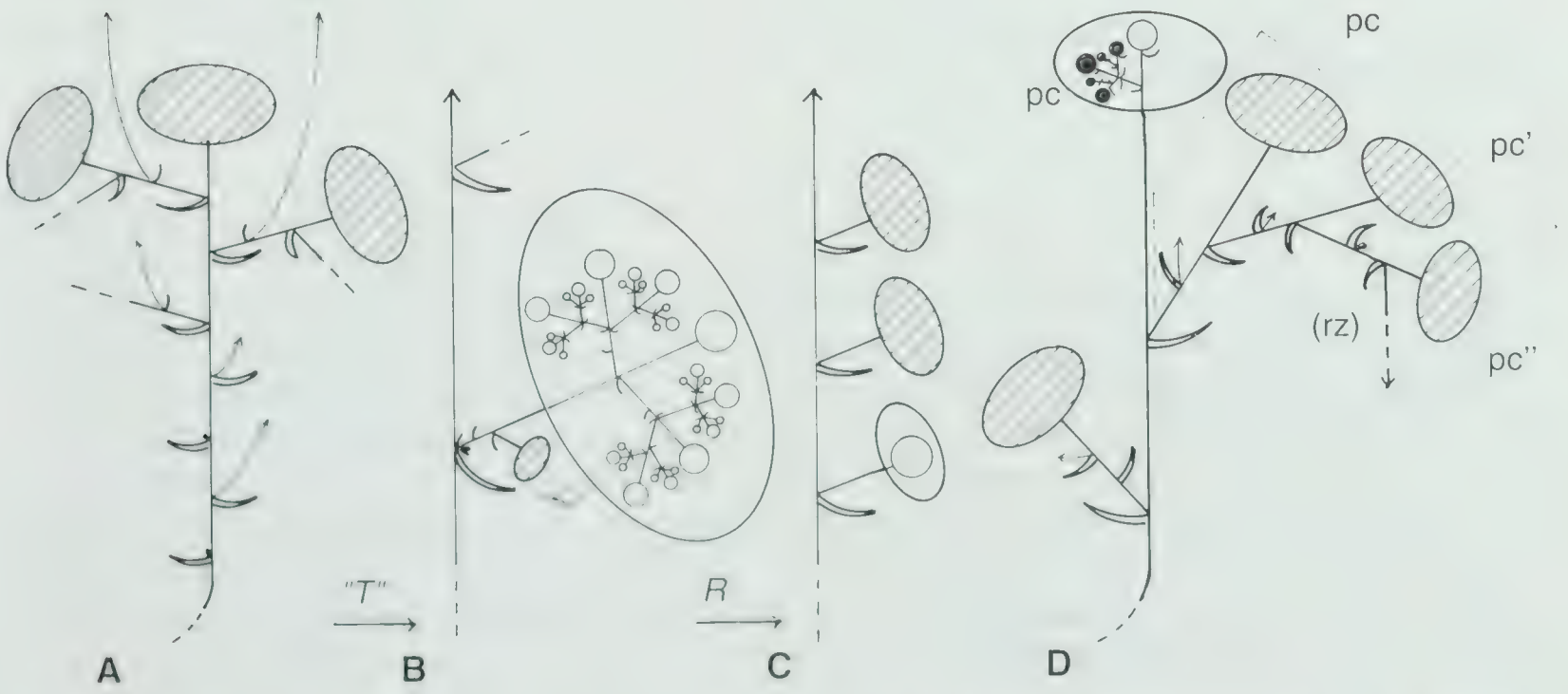


*Figure 217 - **Flowering shoot systems of selected Sterculiaceae** (A,B,D) **and Elaeocarpaceae** (C). A, profile of a flowering innovation shoot of* Abroma augusta *with a terminal and lateral inflorescences, B, structure and lateral position of the so-called `Bicolor-Endverzweigung´ in* Theobroma bicolor, *which is characterized by a terminal flower, one always sterile and two (potentially) fertile bracts subtending cymose partial inflorescences, C, lateral inflorescence in* Sloanea monosperma *being reduced to an axillary flower, D, seasonal growth unit in* Lasiopetalum *sp. illustrating the different paraclades sensu Troll (black/dotted line) and the homology of the lateral flowering sympodia (e.g. pc´, pc´´) with renewal shoots (rz).*

pc, paraclade, R, reduction, "T", truncation (the signs of quotation point to the fact that the process of truncation covers an entire inflorescence instead of a florescence)

A-C, after Bayer (1994), D, after Claßen (1988), all slightly changed.

However he had to accept that the process of truncation (´*T*´´) covers an entire inflorescence instead of a flower or florescence. He furthermore found two types of paraclades, the cymose partial inflorescence of the Bicolor-Endverzweigung (D: black) and the laterally arranged flowering sympodia (D: dotted). Those were so different that Bayer doubted their homology and preferred to restrict the term paraclade to the flowering sympodia. As Claßen (1988) showed in the genus *Lasiopetalum* (D) the elements of the flowering sympodia (pc, pc´, pc´´) are homologous to the renewal shoots (rz) and may merely have developed sylleptically. For that reason she already discussed the problem of the delimitation of the synflorescence, namely whether to restrict the term to the caducous part of the shoot system or to apply it to the whole flowering plant (which starts to flower in the first year in *L. discolor*). The synflorescence in each case represents the monotelic type but is referred to two different levels of organization (compare with fig. 213B,B´). Bayer (1994) finally was confronted with the problem that the transition from a truncate monotelic to a polytelic synflorescence occasionally depends only on the number of flowers within the Bicolor-Endverzweigung, which is generally a highly variable character, but in *Theobroma cacao* varies even within a single individual. Despite these difficulties which Bayer (1994:247-256) himself discussed in detail, he clearly accepted and defended the concept of synflorescences.

Beyond question Troll was an excellent morphologist in terms of analysing and describing botanical structures. However, his scientific interpretations were guided largely by the 'Gestalt' of natural systems (compare with Troll 1925, 1928, 1941). For that reason it is understandable that Troll was impressed by similar patterns and thus preferred the definition of a synflorescence as a system of florescences (B´). But it is hard to understand why his application of the term synflorescence to woody plants has persisted until now in a nearly unchanged version. Of course Troll´s concept was the only typological concept and was successfully tested in several thousand species of annual and perennial herbs, before extended studies of (sub-) tropical trees made the application of the concept dubious. And it was difficult to disentangle the concept of synflorescences from ambuigities and misunderstandings recognizing that analogous patterns do not only appear within caducous synflorescences of different levels of complexity (§ 4.2.3.1), but also between the internal structure of individual synflorescences and their arrangement within more complex shoot systems. Besides there have been only a few critics (Stauffer 1963, Van Steenis 1963), who were largely disregarded and not even cited in the dominant textbook (Weberling 1989):

- Van Steenis (1963) was one of the few contemporary biologist who rejected the application of the term synflorescence to the entire innovation shoot Comparing the inflorescences of *Ananas* and *Sphenoclea* with those of *Melaleuca*, *Callistemon*, and *Pentaphylax* he pointed to the fact that the 'spikes' are only superficially similar. According to him, in the latter examples the 'spike' in fact was the tip of the twig covered with laterally arranged uniflorous inflorescences. Van Steenis accepted vegetative elements within an inflorescence, but he distinguished between ephemeral parts which „*take no part in the extension of structure of the individual mother plant*" (1006/7) (e.g. *Ananas*) and persistent structures which characterize the „*stem-nature of a twig*" (e.g. *Callistemon*). In concluding, he proposed a new definition of an inflorescence as „*the specialized fertile part(s) of an individual plant which post-anthesis does (do) not participate in the vegetative extension of the individual*" (1007) In doing so he agreed with Troll´s second definition of a synflorescence as the flowering shoot system above the renewal zone´.

- More than twenty years later, Schröder (1987) again discussed the question of delimitating an inflorescence in woody plants. He proposed a definition of the term inflorescence which largely correponds to that of Van Steenis: „*Infloreszenz (Blütenstand): ein Teil der Pflanze, dessen Spitzen- und Achselmeristeme in einer Wuchsperiode infolge Blütenbildung sämtlich aufgebraucht werden, so daß er nach der Fruchtreife abstirbt und verloren geht*" *(451).* An inflorescence thus represents a caducous flowering unit that is shed after seed set. In woody plants it is separated from the vegetative-persistent part of the shoot system by the renewal zone. Furthermore Schröder (1987) restricted the ambiguous term 'vegetative' to that part of the plant that survives with active meristems, thus distinguishing between ephemeral and persistent parts

Schröder was the first to note the essential role of the renewal zone in the lower delimitation of an inflorescence in woody plants. But he did not apply his definition of an inflorescence consistently. Though he accepted the term `proliferating synflorescence´ as paradoxical, he approved it in case of e.g. *Lysimachia nummularia*, *Veronica filiformis*, *Callistemon* and *Melaleuca* because of systematic considerations. In doing so he misused inflorescence structures to confirm `clearly known´ homologies (1987:452) rather than to take them as independent data to find out homologies.

As a general conclusion from the discussion of the Trollian concept it appears to be time to reconsider some of its essential elements. It is imperative, if science is to progress, that even widely-accepted theories be re-examined as scientific knowledge expands and new evidence comes to light (compare with Kuhn 1976). This is also true for the concept of synflorescences entrenched in biological thinking for many years.

4.2.3.3 `Uniflorescences´ and `conflorescences´ sensu Briggs & Johnson. Studying the inflorescences in the Australian Myrtaceae, Briggs & Johnson (1979) were confronted with the immense positional variability in flowering woody plants. They examined Troll´s concept of synflorescences, but rejected it for both practical and theoretical reasons. They objected in particular to the application of the terms `synflorescence´ and `main florescence´ to woody plants and the term `prolification´ „*which may suggest that a perennial condition for a flowering axis is considered somewhat aberrant*" (236). Like Parkin (1914; fig. 205) and Van Steenis (1963) they pointed to the analogous nature of `racemes´ being formed either by aggregation of lateral units or by truncation of the terminal unit. They rejected on principle the typological method used by Troll because they considered the underlying assumptions to be arbitrary and idealistic and thus not to be appropriate to reflect phylogenetic relationships. A further reason might have been that Briggs & Johnson (1979) proceeded from a systematic point of view and therefore looked for simple and discrete characters (compare with Pankhurst 1984). Troll in contrast typified complex entities. He interpreted the types in an idealistic manner. This might be refused, but not typification which like classification is a fundamental empiric procedure to characterize diversity. On principle, it always depends on the underlying question which data (simple/complex) and procedures (classification/typification) were selected. In this respect systematics and morphology differ in a complementary manner. By rejecting typological concepts it is often overlooked that typology is not an inadequate procedure but only appears to be inadequate for systematic, particularly cladistic purposes (Claßen-Bockhoff 1999).

Briggs & Johnson (1979) introduced a strictly descriptive terminology for comparing the inflorescences in different arborescent species (fig. 218).

- As a reference framework they used the `seasonal growth unit´ (SGU) i.e. a „*shoot, or branched system of shoots, formed within a single growing season and arising (terminally or laterally) from an axis formed in a previous growing season*" (175). The SGU (which is also used in § 3) corresponds largely to the `Schub´ sensu Pilger (1922) and the flowering innovation shoot sensu Troll (1964).
- Shoots ending in a terminal flower were called `anthotelic´ (a), whereas those with a vegetative tip were called `blastotelic-auxotelic´ (au) in case where the apex continues to grow and `blastotelic-anauxotelic´ (an) in case where the apex dies off. The terms differ from Troll´s concept of monotely and polytely in being `theory-free´ i.e. related to any shoot within the SGU and not only to the main axis and do not imply any phylogenetic derivation. Blastotelic and in particular auxotelic shoot tips are thus not necessarily secondary products which appear only after truncation and prolification, but may equally or even in the mayority of cases represent a primitive condition. Following Briggs & Johnson (1979) the primitive condition in woody plants might have been characterized by a certain flexibility between anthotely and blastotely which is still present in some living Myrtaceae: „*In these, when a shoot comes into the flowering stage, the shoot apex may possess the potential either to produce vegetative growth or to terminate in a flower*" (187). Proceeding from such a flexible condition, Briggs & Johnson (1979, 1982) derive the more stablilized condition of a strictly lateral or terminal position of flowers.

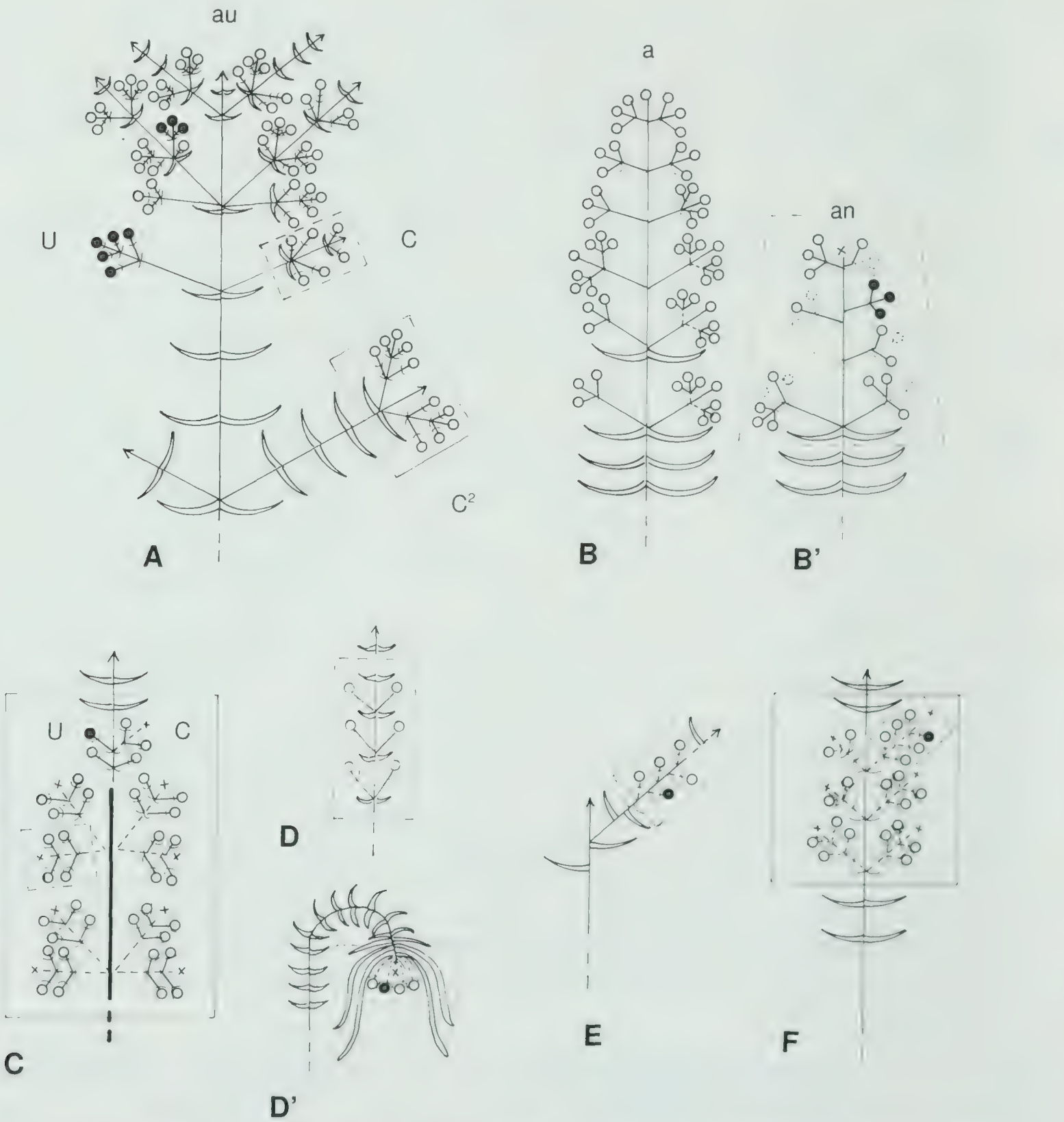


*Figure 218 - **Flowering shoot systems of selected Myrtaceae** illustrating the terminology of uniflorescences (U; black), conflorescences (C; dotted lines) and superconflorescences (C²; black lines) used by Briggs & Johnson (1979). Profiles of A,* Decaspermum paniculatum, *B,B',* Angophora *sp., C,* Eugenia *sp., D, D',* Darwinia *sp., E,* Callistemon *sp., F,* Melaleuca *sp. The reference unit is the seasonal growth unit (SGU). The shoot tips are blastotelic-auxotelic (au), blastotelic-anauxotelic (an) or anthotelic (a). Note that the concept is not applicable to determinate SGU's (B) and that the flexible condition of the apices result in a different terminology (A,C: U, C). After Briggs & Johnson (1979), redrawn and slightly changed.*

- As regards inflorescences Briggs & Johnson (1979) introduced the terms uniflorescence (U) for characterizing an anthotelic branch system within a SGU that is lateral to a blastotelic axis (or, more generally, a floriferous branch system qualitatively different from the axis on which it is borne) and conflorescence (C) for characterizing a floriferous branch system of which the main axis bears U's. Functional aggregates of C's which belong to the same or different SGU's are called superconflorescences (C²) The three introduced terms represent different levels of complexity. The uniflorescence is the smallest flowering unit, which is always laterally arranged, determinate and caducous. Briggs & Johnson (1979) applied the common terms of inflorescences, e.g. panicle, botryoid, monad to this level of organization By contrast conflorescences are terminally or laterally arranged, always indeterminate and thus principally capable of becoming auxotelic Phylogenetically they may either reflect a primitive condition or may be derived from uniflorescences by truncation.

To distinguish the two levels of organization Briggs & Johnson (1979) used modified terms as e.g. racemiform and thyrsiform to describe the arrangement of U´s within a conflorescence. The superconflorescence finally represents the largest flowering unit including any compound cluster of conflorescences.

Applying the new terminology to the flowering shoot systems in Myrtaceae Briggs & Johnson (1979) were obliged to make some restrictions. Particularly, the terms appeared to be inapplicable to those taxa in which the anthotelic or blastotelic condition of a shoot tip is not fixed but flexible (fig. 217A,C: U, C) or where the main axis of the SGU ends in a flower, *„since the whole inflorescence is in some ways equivalent to a uniflorescence, whereas in other respects its lateral branches resemble uniflorescences"* (1979:177; fig. 218B). Apart from these exceptions the terms were reliable for describing the flowering shoot systems in Myrtaceae. As fig. 218C illustrates lateral kataleptic flowering shoots represent individual SGU´s and thus the terms are also applicable to cauliflorous species. As a consequence of the strictly descriptive nature of the terms, many monadic and triadic uniflorescences appear within the Myrtaceae. Furthermore it has to be accepted that an uniflorescence abruptly changes into a conflorescence as soon as the terminal flower is lacking (fig. 218A,C: U, C) and that all indeterminate inflorescences represent conflorescences independent of their being caducous or not.

Being theory-free and strictly descriptive, the concept of Briggs & Johnson represents the direct opposite of the typological concept of Troll. It is applicable to many flowering shoot systems, but prompts certain questions such as: Are uniflorescences comparable to the entire inflorescence of determinate SGU´s or are they part of them (fig. 217B,B´)? Are lateral shoots arising from the same node comparable to each other, regardless of whether they bear uniflorescences or conflorescences (fig. 217A,C)? Though the concept itself is consistent, it admits no typological comparisons and for that reason is not appropriate for inflorescence morphology. Despite this criticism, it is acknowledged that Briggs & Johnson (1979), however, made an important contribution to the understanding of inflorescence morphology. By proceeding from vegetative shoot systems and by pointing to both the flexible condition of the shoot tip and the analogous nature of `racemes´, they reconsidered the term `prolification´.

4.2.3.4 `L´unité de floraison´ sensu Sell. In contrast to the typological concept of Troll (§ 4.2.2.1) and to the descriptive approach of Briggs & Johnson (§ 4.2.3.3), Sell (1995) presented a physiological view of inflorescence evolution. He was less interested in individual phylogenetic lines than in the superior evolutionary tendencies which appear as parallelisms all over the Angiosperms. In a study of compound inflorescences in various Angiosperm families (e.g. Sell & Cremers 1992, 1994), Sell found that the `florescence´ sensu Troll and the `uniflorescence´ sensu Briggs & Johnson did not represent his evolutionary and morphogenetic view. He therefore searched for the definition of a fundamental flowering unit (`unité de floraison´, UF) which should characterize the smallest flowering pattern of a species and be repeated within the shoot system as a morphogenetic entity. Attaching more importance to function than to structure, he defined his reference unit by both structural and functional characters: *„L´unité de floraison est un système sylleptique plus ou moins ramifié, réitératif et caduque, exprimant les potentialités reproductrices minimales d´une unité de croissance saisonnière et traduisant l´aboutissements du fonctionnement d´un méristème unique après maturation et induction florales"* (Sell 1995:374). Following this definition, the UF corresponds to a spike-like inflorescence in Marantaceae (fig. 219), to an umbel-like thyrse in Euphorbiaceae, to a head in Asteraceae and to a spikelet in Poaceae, thus to `pseudoflorescences´ sensu lato which are regulated by the plant as morphogenetic units (Sell & Cremers 1992, 1994).

Sell (1982) illustrated that the flowering units which often appear as subunits in compound inflorescences were produced by the elementary processes of inflorescence evolution, particularly homogenization and truncation. He showed that, in the racemose members of the Myrtales, these processes affected different levels of complexity and that the size of the original inflorescence determined whether the product would be a simple (e.g. Myrtaceae, Onagraceae), double (e.g. Myrtaceae, Lythraceae, Combretaceae) or triple raceme (e.g. Myrtcaeae, Combretaceae). Thus, by

means of homogenization and truncation the original paniculate structure of a flowering shoot system would be changed into a racemose one, better corresponding to the modular growth of the plant body.

As Sell defined inflorescences as caducous structures (e.g. 1995:372) he consequently had to distinguish two levels of complexity in woody plants, the individual caducous inflorescence and the series of such inflorescences. *„Bis jetzt wurden nur die Rispen selbst in Betracht gezogen, als wären sie alleinstehend,... Dennoch gibt die Beobachtung vieler, zu den Myrtalen gehörenden Arten zu erkennen, daß sehr oft solche Rispen sich in einer ununterbrochenen Serie am Ende der Sprosse einordnen, wobei jeder dieser Sprosse von einer Rispe gekrönt oder nicht gekrönt sein kann.*"(1982:400). He showed that the elementary process of homogenization also affected the more complex level of inflorescence aggregates (*„Blütenstandsaggregate*", Sell 1982:400), whose serial arrangement was itself interpreted as being a product of homogenization. He thus demonstrated the independence of the process of homogenization from any structure and life form of the plants.

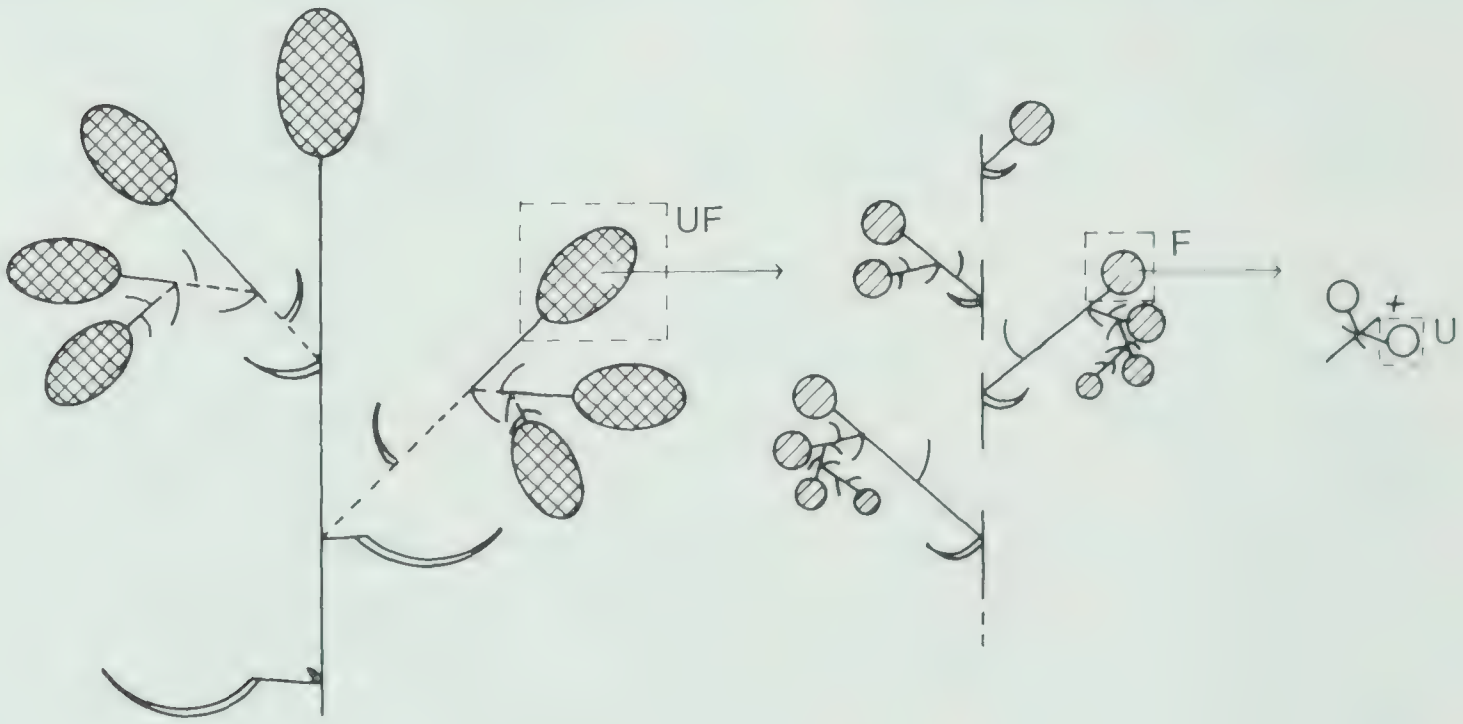


Figure 219 - **Ischnosiphon arouma *(Marantaceae).*** *Profile of an inflorescence composed of spike-like units, each composed of drepania bearing diads. Note that the florescence (F) sensu Troll corresponds to a diad, the uniflorescence (U) sensu Briggs & Johnson to a flower and the unité de floraison (UF) sensu Sell to a spike-like inflorescence. After Sell & Cremers 1994, (compare with Kunze 1985).*

Consequently, racemes in woody plant families may result from two different evolutionary pathways *„Man kann darauf hinweisen, daß offene Trauben (einfache oder zusammengesetzte) auf zwei verschiedenen Wegen zustandekommen können: entweder durch Trunkatur einer geschlossenen Traube ... oder direkt, von einem prolifierenden Sproß aus, nach Homogenisierung der achselständigen Rispen ...*" (1982:408). Fig. 220 illustrates such an example in the Myrtaceae. The racemes in *Eugenia* and in *Eucalyptus* were both produced by homogenization, but in *Eugenia* the raceme originated from a caducous terminal panicle (black) and in *Eucalyptus* from a series of reduced panicles (sciadioids) being arranged on a woody shoot (white).

As regards the apex of flowering woody shoot systems, Sell (1982:409) accepted both determinate and indeterminate shoots. He was less interested in deriving the one from the other than in explaining the underlying physiological processes. Studying floral monopodes', flowering accessory shoots, anisoclady and reiterative prolifications' he concluded that the apical meristem might be subdivided into different sectors each determining either a floral or a vegetative organ: *„Au niveau du méristème édificateur, il convient toutefois de reconnaître, lors de la mise en place des organes reproducteurs latéraux, la coexistence d'un territoire à activité florale et d'un territoire conservant ses potentialités végétatives*" (Sell 1995:386). Proceeding from a biological viewpoint, Sell (1995) pointed out that all organisms are subject to exogenous stimuli and endogenous rhythms in space and in time. He therefore positively expected intermediate structures (e.g. anisoclady) and rhythmic repetitions (e.g. proliferations).

For the present investigation it is noteworthy that Sell (1) defined inflorescences as caducous units, and in so doing (2) distinguished two levels of organization in woody plants. He (3) showed that both, the caducous inflorescence and the aggregate of inflorescences, are regulated by the same physiological processes. He (4) introduced a morphogenetic view into inflorescence morphology, pointing (5) to the regulation of biological entities, (6) the supposed sectorial subdivision of the apical meristem, (7) the appearance of intermediate structures and (8) the plant´s capacity to react in a flexible manner.

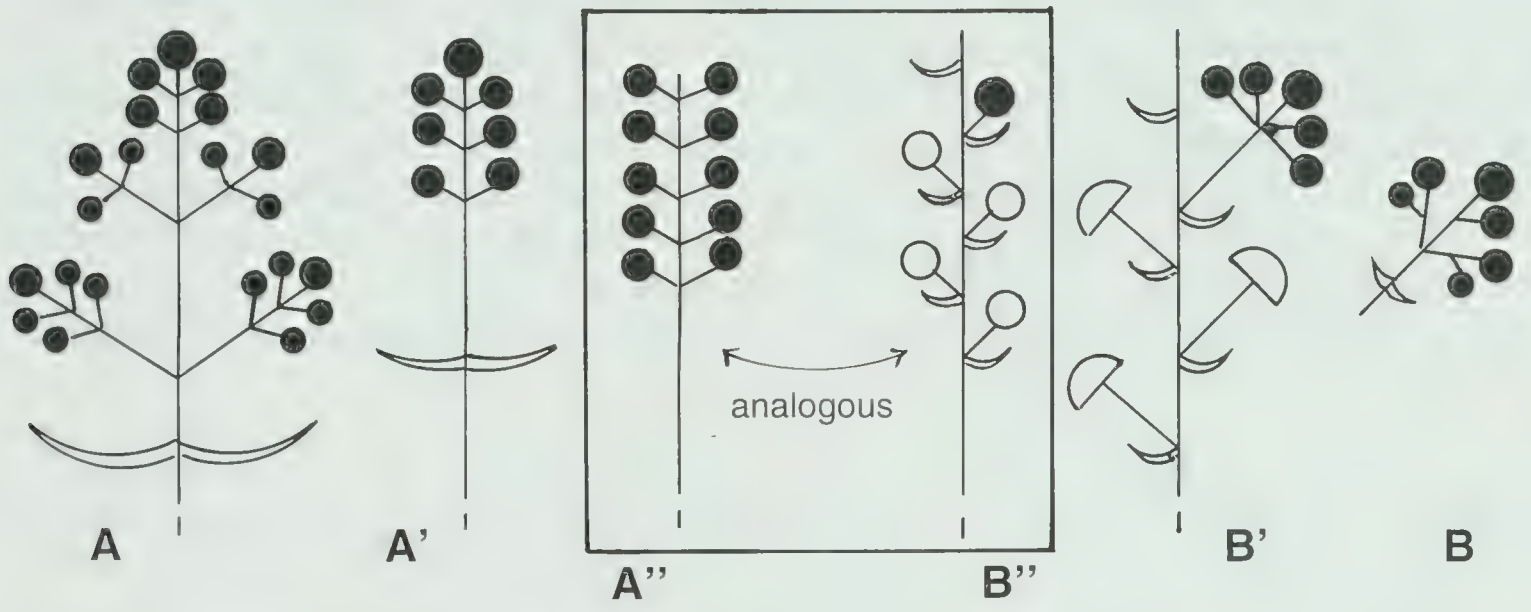


Figure 220 - ***Formation of racemes in Myrtaceae*** *by different evolutionary pathways: A-A´´, homogenization of an individual panicle in* Eugenia, *B-B´´, homogenization of a series of axillary panicles in* Eucalyptus. *A-A´´, terminal panicles of A,* Eugenia aromatica, *A´,* E. jambos *(syn.* Jambosa vulgaris*), A´´,* E. dasyantha, *B, reduced axillary panicle (sciadioid) of* Eucalyptus ficifolia, *B´-B´´, series of axillary sciadioids of B´,* E. *sp. and B´´,* E. globulus. *Black: caducous inflorescence, white: woody shoot system bearing inflorescences After Sell 1982.*

In defining his reference unit as a pattern instead of a clearly defined structure, he left the typological base for homology. He could therefore largely ignore the terminological demands of comparative morphology, terming each racemose structure a `raceme´. In fact Sell never used the terms homology and analogy as representing different evolutionary pathways, but merely pointed out that only the analysis of the entire taxonomic group would permit the identification of the origin of a `raceme´.

4.2.4 Architectural studies in woody plants.

An investigation of inflorescences in woody plants may proceed along two lines: inflorescence and growth form morphology (see fig. 271). Though both disciplines meet in the analysis of flowering woody shoot systems the procedures are different - as Parkin (1914) and Pilger (1922) demonstrated in the early part of this century. Parkin (see § 4.2.1.1) proceeded from a shoot tip that starts to flower and is enriched basipetally by axillary flowers. He thus concentrated upon strictly reproductive shoot systems irrespective of the growth form of the plant. Pilger (see § 4.2.1.2) in contrast proceeded from a vegetative shoot system starting to produce flowers at the end of different shoots. Recalling the longitudinal gradient discussed by Sell (§ 4.2.2.2), Parkin held the view that the flowering impulse extends basipetally from the apex while Pilger held that the vegetative vigour is always present in woody shoot systems. Both views coincide when the production of terminal inflorescences (sensu Parkin) is projected into a branched seasonal shoot system (sensu Pilger).

The preceding chapters (§ 4.2.2 - § 4.2.3.4) have illustrated the historical development of the most important concepts of inflorescence morphology in recent decades. It was shown that the perennial life form of woody plants and the presence of overground renewal shoots within the flowering canopy rendered morphological analysis more difficult than in annual plants. Different definitions for the flowering reference unit were given (`synflorescence´, `inflorescence´, `uniflorescence´, `unité de floraison´), each resulting in a different interpretation of what constituted an inflorescence in woody

plants. The terms which were applied to woody shoot systems bearing exclusively lateral inflorescences (`intercalary inflorescences´, `proliferating synflorescences´, `conflorescence´, `inflorescence aggregate´) indicate that the investigations related more to inflorescences than to perennial shoot systems.

The main problem appears to have arisen from a failure to distinguish between the two levels of complexity, the caducous inflorescence and the perennial shoot system, the latter being the subject of growth form morphology. Though inflorescence and growth form morphology may analyse the same flowering shoot systems, the reference units and consequently the conclusions reached are different for the two disciplines. In growth form morphology the architecture of the plants is paramount, the reference system being a distinct shoot system (see § 4.2.4.2) and no longer an inflorescence.

Historically, growth form morphology was a by-product of geography, going back to the times of Humboldt´s `Ideen zu einer Physiognomik der Gewächse´ (1806). Later, Troll (e.g. 1937) and Rauh (e.g. 1939) established it as a separate biological discipline which was continued mainly by Meusel (e.g. 1951) and his school (for literature see Hagemann 1989). A new initiative was set up by the school in Montpellier. Hallé, Oldeman & Tomlinson (1978) presented architectural models for tropical trees which were used as references in many studies relative to tropical and temperate trees, lianes and shrubs (e.g. Cremers 1974, Edelin 1977, 1991, Barthélémy 1988, Gleißner 1998).

4.2.4.1 Longitudinal symmetry and the position of inflorescences. As regards inflorescences in woody plants, the main question concerns the structural preconditions necessary such that a vegetative shoot system may produce flowers when changing from juvenility to maturity.

- Goebel (1928) introduced the term `longitudinal symmetry´ to describe the influence of the shoot polarity on the development of lateral shoots. Acrotony usually appears in woody plants of temperate climates in which lateral shoots develop cataleptically; in contrast mesotony most often characterizes the syllepticaly branched shoot systems of woody plants in warmer climates (fig. 221A,B) As regards the evolution of different symmetries, Troll (1937:607) supposed that acrotony may have evolved from mesotony by inhibition of the upper part of the longitudinal period.

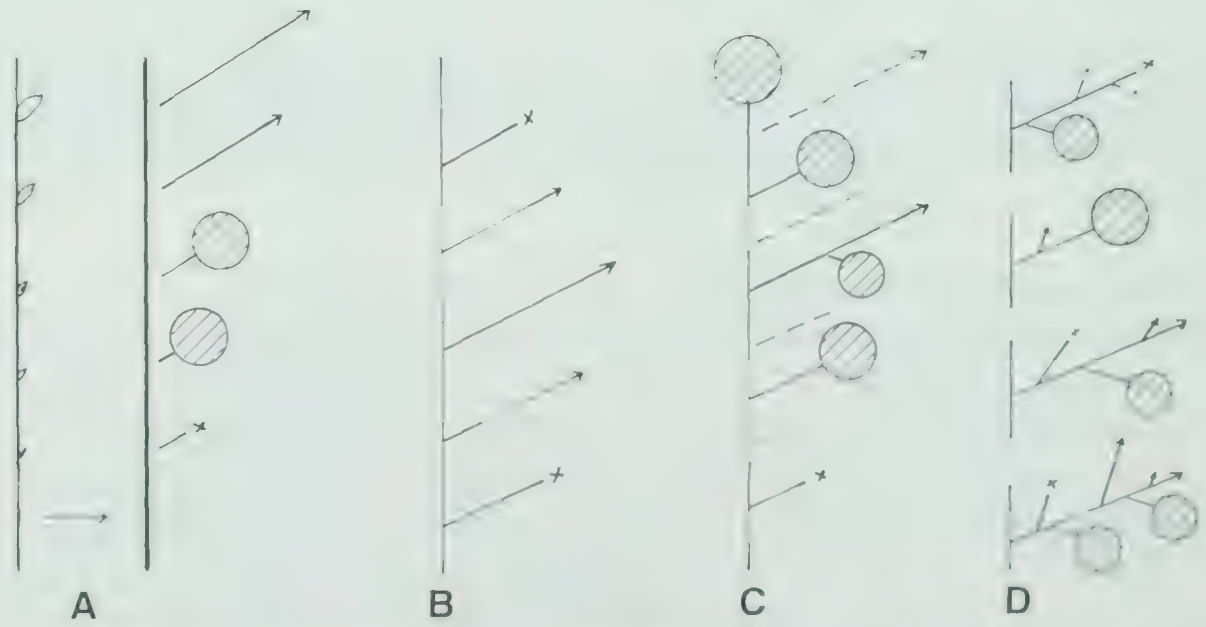


*Figure 221 - **Longitudinal symmetry in woody shoot systems**. A, cataleptic acrotonic behaviour characterising trees in temperate climates, B, sylleptic mesotonic behaviour characterizing trees in warmer climates, C, example showing the superposition of the two gradients, D, examples showing the variation of lateral shoots dependent on their relative position and vegetative vigour (the position of the inflorescences reflects the view of Hauser 1932).*

- Hauser (1932) concluded from his studies on gymnospermous and angisospermous trees that branching behaviour and capacity to produce flowers are directly influenced by the position and thus by the vegetative vigour of the lateral shoots concerned. As a general rule he argued that both the most vigorous and the weakest shoots would remain in a vegetative state, in the first case continuing the perennial shoot system and in the second case dying off. Only the shoots of moderate vigour would be able to produce flowers (fig. 221D)

The example of *Betula humilis* (fig. 222) illustrates his view. Short shoots terminate in a male catkin (hatched) and remain unbranched (G) or bear a few sylleptic (in Hauser's terminology: proleptic) lateral shoots. These end in male catkins (F), the most vigorous (E) being able to produce lateral female catkins (black) which develop the following spring. In contrast, long shoots (B) tend to end vegetatively and often bear sylleptic lateral shoots characterized by mesotony (arrows). The most vigorous ones terminate vegetatively while the second most vigorous branches terminate in male catkins as do the weakest which however bear only bracts instead of foliage. Female catkins, which become dormant and develop the following spring, are formed above and below the zone of sylleptic lateral shoots. The sylleptic lateral shoots repeat the branching behaviour of the parent axis, producing female catkins in the same manner. Hauser (1932) illustrated variation to the general rule, showing (1) that the position, number and sex of the catkins depend directly on the degree of vegetative vigour of both the parent and lateral shoots (A-G) and (2) that the superposition of acro- and mesotony may result in an intermediate pattern (D; fig. 221C,D).

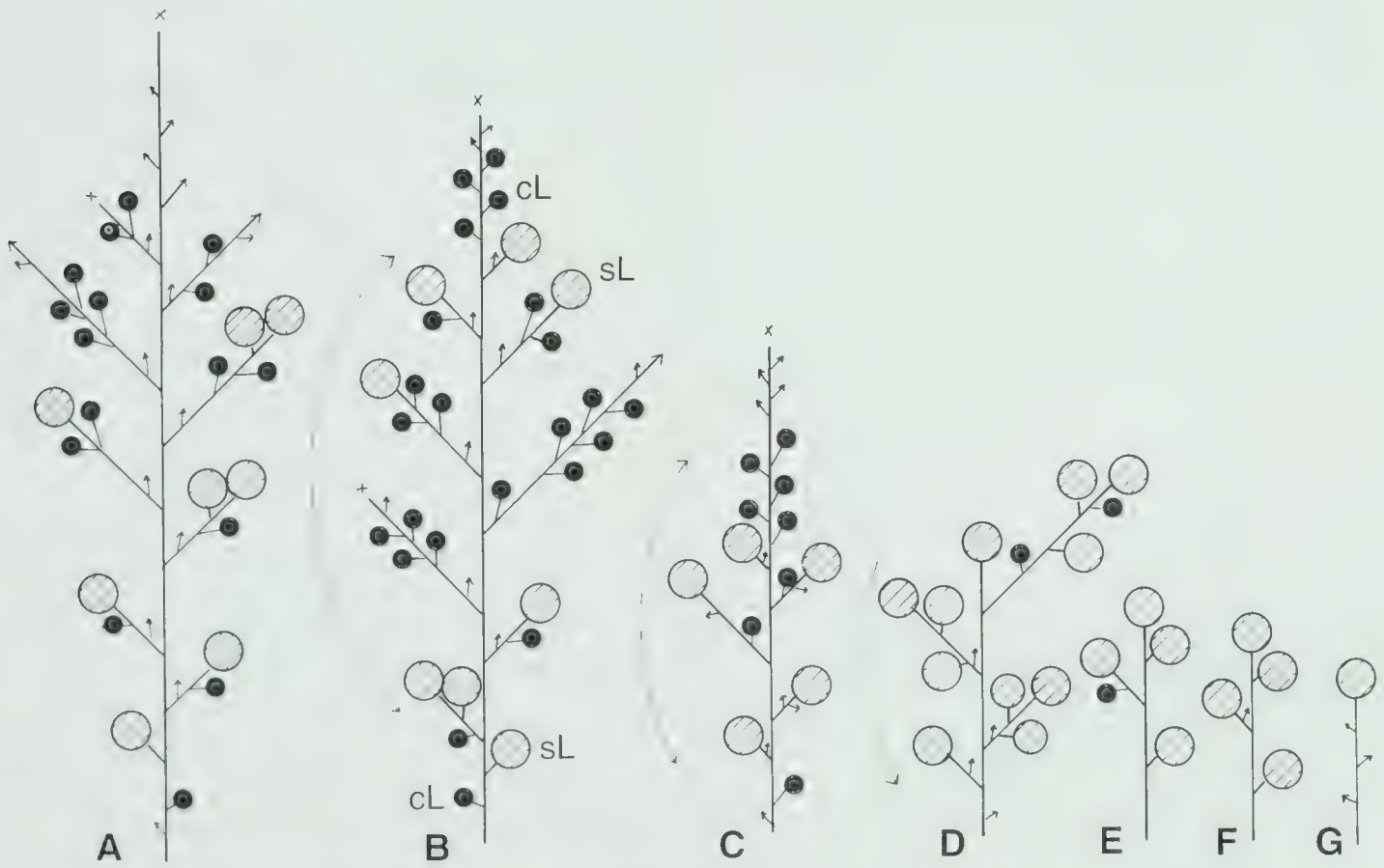


*Figure 222 - **Flowering shoot systems in** **Betula humilis** illustrating that the number and sex of floral shoots depend directly on the vegetative vigour of the shoot system. A-C, long-shoots, B, the most characteristic one showing mesotonic sylleptic branching. Note that the most vigorous sylleptic lateral shoots are indeterminate and that the remaining sylleptic shoots end in male catkins (A,B). Both are capable of producing axillary female buds, thus repeating the behaviour of parent axis in bearing female buds at its weakest basal and apical parts. D-G, short, determinate, predominantly reproductive shoots, in D with an unusual acrotony, perhaps indicating the superposition of two different longitudinal gradients*

cL, cataleptic lateral shoot, sL, sylleptic lateral shoot;
the arrows indicate the decreasing vigour of the lateral shoots;
hatched: male catkins, black: female hibernating buds,
Slightly changed after Hauser 1932.

- Schutzsack (1965) studied flowering rhythms in Hamamelidaceae, namely (1) the time and duration of anthesis in fall/winter, spring and summer blooming species, (2) the time of production and development of vegetative and floral buds, and (3) the position of floral buds within a seasonal shoot system. He found e.g. in *Hamamelis virginiana* that floral buds were formed throughout the year but did not come to flower before autumn when all were synchronously stimulated by temperature. In order to explain the different length of the dormancy period between the early and the late buds, Schutzsack distinguished morphogenetic (floral bud formation) and physiological (stimulation by temperature) developmental stages.

Like Hauser (1932), Schützsack argued that a one season old vegetative shoot system gradually changes to become reproductive. Fig. 223 illustrates the transition from the vegetative to the reproductive stage in *Hamamelis virginiana*.

(1) The vegetative stage is characterized by indeterminate 'vegetative, branched long-shoots' which show the most vigorous lateral shoots at the base (A). Schützsack distinguished the vegetative branched (v1), the vegetative unbranched (v3) and the transitional zone (v2) and showed that zone v1 and v2 may be reduced leaving only zone v3 characterizing an 'unbranched vegetative long-shoot'.

(2) The early reproductive stage is represented by unspecialized 'vegetative-reproductive, branched long-shoots' (B) which is subdivided into a reproductive proximal (r1-r4) and a vegetative distal part (v2-v3). Within the reproductive region the vegetative vigour of the lateral shoots decreases form the base (r1) upwards, losing first the terminal vegetative bud and the foliage (r2) and then the branching capacity (r3,r4).

(3) The reproductive stage is characterized by increasing reduction and specialization (C-E) The vegetative zone is confined to the distal zone (C), then to the terminal vegetative bud (D) and finally disappears completely, leaving a caducous shoot system (E). In the latter case the shoot system is renewed by long-shoots arising from axillary shoots of preceding unspecialized shoot systems.

*Figure 223 - **Transition from vegetative to reproductive shoot systems** in* Hamamelis virginiana. *A, branched vegetative long-shoot, B, branched reproductive-vegetative long-shoot representing the early reproductive stage, C-E, branched reproductive short-shoots showing the gradual decrease of vegetative vigour. Note the strict reproductive nature of E. v1-r4, vegetative and reproductive zones of a one season old shoot system: v1, vegetative branched zone, v3 vegetative unbranched zone, v2, intermediate zone between v1 and v3; r1, r2, reproductive branched zones with (r1) and without (r2) a terminal vegetative bud, r3, r4, reproductive branched (r3) and unbranched (r4) zones with largely inhibited vegetative shoots Black: vegetative leafy shoots, dotted: reproductive bracteate shoots. After Schützsack 1965, slightly simplified for greater clarity*

In summary, Schützsack demonstrated that the number and position of the floral buds in *Hamamelis virginiana* depend directly on the vegetative vigour of the shoot system concerned. He thus extended Hauser's theory by illustrating the gradual change from strictly vegetative to strictly reproductive shoot systems with increasing age of the plant.

The examples (fig. 222, 223) show clearly that the position of inflorescences in woody shoot systems depends upon the age and branching pattern of the underlying vegetative shoot system and that it is scarcely possible to interpret the flowering patterns of woody plants solely on the basis of inflorescence morphology.

4.2.4.2 Architectural models, constructional units and the concept of neoteny. Hallé et al. (1978) published the first textbook that provided an overview of the problems inherent in the study of woody plants. These took a dynamic view and interpreted a tree as a changing entity. They described the `architecture´ of a tree, that is the *„visible morphological expression of the genetic blueprint of a tree at any one time*" (1978:75) in terms of `models´ representing the growth program of a tree changing with time. Hallé et al. (1978) recognized twenty-four models in the pantropical rain forest and illustrated each with a series of figures (fig. 224).

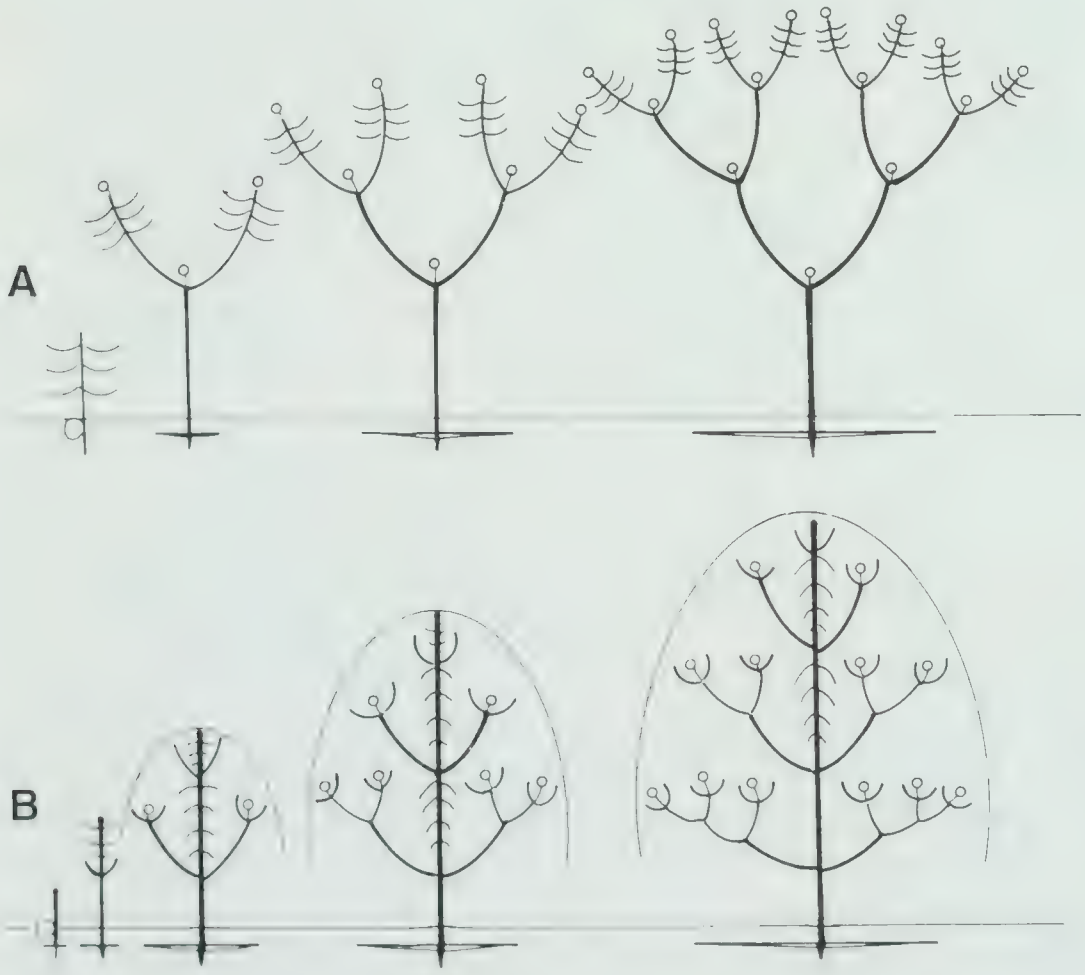


*Figure 224 - **Series of figures of selected architectural models** illustrating the changing nature of the plant´s architecture. A, Leeuwenberg´s model, B, Scarrone´s model*
After Hallé et al. 1978.

In order to identify the architecture of a given plant, it was necessary to study both its growth rhythm and its branching pattern in time. Hallé et al. (1978) presented a broad discussion of the relevant terms and phenomena, e.g. the phases of development in a growing plant, rhyrhmic/continuous growth, monopodial/sympodial shoot connection, syllepsis/prolepsis (= catalepsis in the present paper), orthotropy/plagiotropy and shoot differentiation, including increasing specialization.

As regards the present investigation, two aspects are of special interest, namely (1) the definition of elementary units of construction and (2) the role of inflorescences relative to architectural models:

ad 1 Proceeding from a developmental view Hallé et al. (1978) distinguished three constructional units:

- the unit of extension (UE; originally defined by Hallé & Martin 1968) *„which is usually detectable on the shoots of trees and shrubs, either in tropical or extratropical climates, as the length of vegetative shoot between two successive groups of bud scale scars*" (Hallé 1986:77) (fig. 225C),
- the unit of morphogenesis (UM) which is the *„length of vegetative shoot whose chronological limits are determined by a single period of continuous activity of the apical meristem*" (Hallé 1986:77) (fig. 225B) and

- the module which is „*the leafy axis in which the entire sequence of aerial differentiation is carried out, from the initiation of the meristem that builds up the axis to the sexual differentiation of its apex*“ (Hallé 1986:78) (fig. 225A).

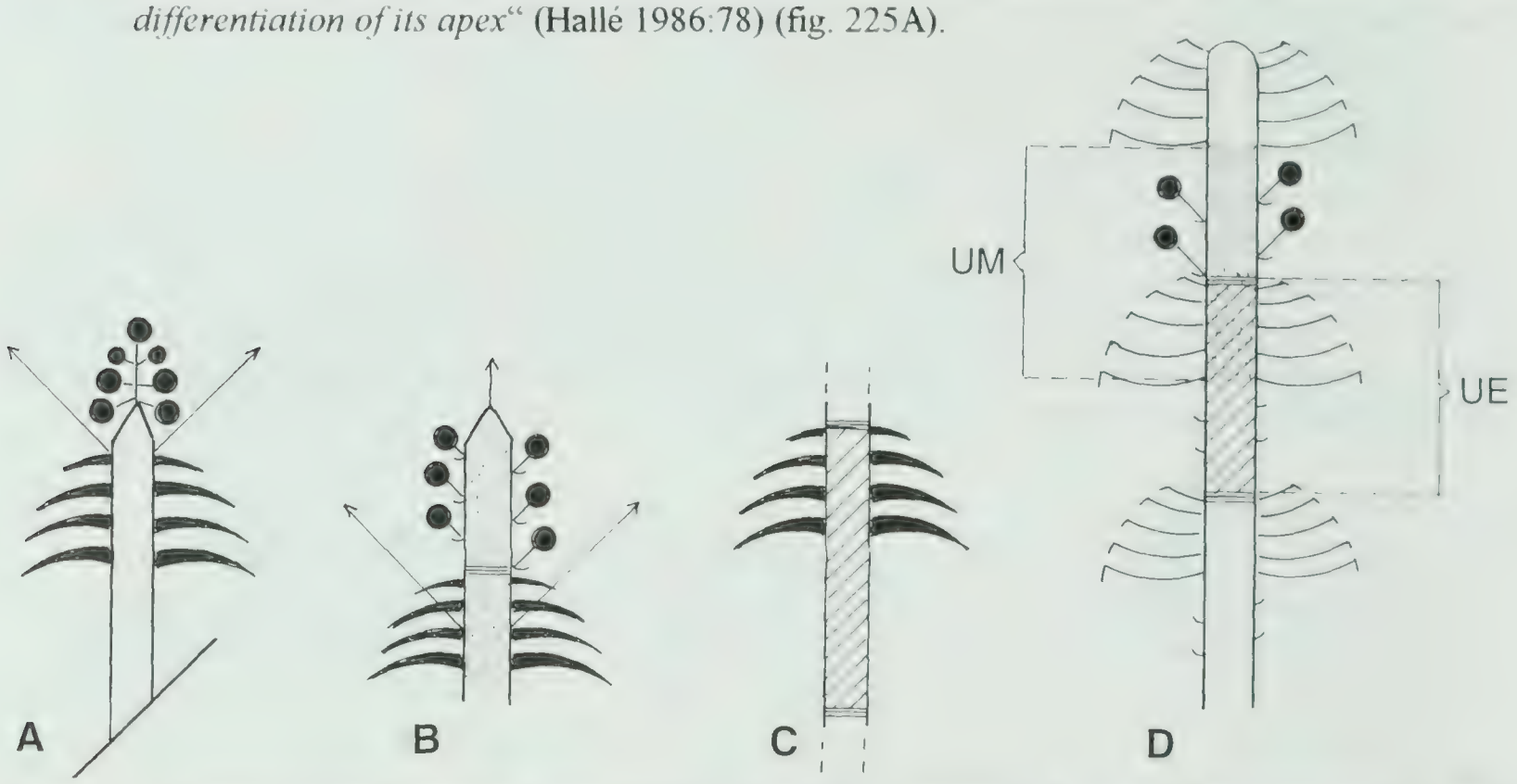


*Figure 225 - **Constructional elements** sensu Hallé et al. (1978). A, module, B, unit of morphogenesis, C, unit of extension, D, schematic profile of the monopodial shoot system of* Hevea brasiliensis *illustrating the different meaning of `unit of extension´ (UE) and `unit of morphogenesis´ (UM).*
A-C, after Hallé 1986, D, after Hallé et al. (1978).

The term `module´ represents a translation of the French term `l´article´ introduced by Prévost (1967) and corresponds largely to the term `sympodial unit´ (Bell 1991), though the latter has a less developmental definition. The term `unit of extension´ refers to the growth rhythm of a monopodial shoot chain and often coincides with an individual SGU. It may or may not correspond to the `unit of morphogenesis´ which characterizes the time of meristematic activity. *Hevea brasiliensis* (fig. 225D) gives an example for the case where the cycle of shoot extension is not congruent with the cycle of initiation. The latter lasts from the middle of the previous UE until a late bud stage that externally resembles dormancy, but in fact is concerned with initiation of the foliage of the following UE. Further examples are known particularly from floral phenologies, e g when flowers are initiated in summer or fall, then overwinter (naked or in buds) and do not flower before next spring (compare with fig. 216, 222).

Unfortunately Hallé et al. (1978) did not explain the relationship between the constructional units. Obviously, UE and UM are both units of time, the UE being influenced by external conditions, while the UM is regulated endogenously. The module, in contrast, seems to be a time-independent unit of organisation. It is not clear whether the authors would agree that a module developing in a single stage corresponds simultaneously to an UE or UM. It is also not clear whether the UM represents at the same time a unit of organisation, similar to module, but applicable to monopodial shoot chains only. Besides, the costs of identification of the individual constructional units are not comparable, usually being easy in sympodial and much more laborious in monopodial systems. As limited knowledge exists about the physiology of buds, it will be necessary in future to intensify studies in this field to obtain more clarity about the mitotic active periods in buds and the resulting periodic and continuous growth rhythms.

In the present context it is necessary to single out to two important consequences of comparing the units UE and UM.

- Floral elements that are preformed in terminal buds occupy a terminal position relative to the UM concerned, but may appear at the base of the following UE (fig. 225D). In this case, the position accorded to the floral elements will depend on which reference unit is selected

- Plants which have continuous meristematic activity e.g. palms, may also show distinct flowering periods. In such groups, a rhythm induced by exogenous stimuli will be superimposed on the endogenous developmental programme.

The central issue may be summarised in the question: which is the most appropriate reference system for the identification of individual inflorescences in woody plants? The developmental pathway is clearly a natural construct but is usually not known. On the other hand, inflorescences referred to the unit of extension, while apparently easily identified entities, may turn out to be artificial constructs. Thus, it might be favorable to find out a reference system that allows comparison of inflorescences in a time-neutral manner.

ad 2: The views of Hallé et al. (1978) regarding inflorescence morphology are essentially superficial. In their view only the position (and not the structure) of the inflorescences may influence the architecture of the tree, particularly when inflorescences appear terminally and force sympodial growth. Hallé et al. (1978) therefore distinguished only two ontogenetic conditions relative to flower formation: hapaxanthy, characterizing vegetative shoots with a terminal flower/inflorescence, and pleonanthy, characterizing indeterminate vegetative shoots bearing flowers/inflorescences in a lateral position.

However, they also discussed some fundamental aspects of inflorescence morphology.

- They proposed substituting the term `inflorescence´ with the term `axis at inflorescence´ to draw attention to the dynamic nature of flowering.
- They found the term `inflorescence´ to be artificial as applied to many woody plants e.g. Myrtaceae,
  (1) where the terminal position of the inflorescence might become subterminal with increasing growth activity of the apex (e.g. *Callistemon*),
  (2) where inflorescences were found both at the base of long shoots and at the apex of short shoots,
  (3) where solitary axillary flowers might be arranged at both a perennial and a caducous shoot within the same individual,

thus, where hapaxanthy and pleonanthy appear at the same individual.

- The significance of Hallé et al.´s contribution lay in their application of the concept of neoteny (see Takhtajan 1973, 1976) to flowering shoot systems. According to Hallé et al., the entire life cycle of a tree from the juvenile stage to senescence, is characterized by an increase in ontogenetic abbreviations: the length of individual internodes decreases with age as does the length of the UE´s and the general branching capacity. Finally, only miniaturized models of the plant´s architecture appear at the periphery of the flowering canopy, illustrating the minimal developmental programme (Barthélémy 1988, Gleißner 1998). The decrease in vegetative vigour is accompanied by an increase in sexuality. The weaker lateral shoots are first influenced by the reproductive impulse, followed by the apex of the main shoot, which would then also be terminated by a flowering unit. Hallé et al. (1978:260) interpreted this terminalization as a precocious expression of sexuality comparable to the zoological examples of foetalization. They concluded that the rapid sexuality of herbs whereby most or all of the aerial axes are involved might be likewise caused by neoteny.

Barthélémy (1988) largely confirmed the general statements of Hallé et al. (1978) in a study of the onset of sexuality in tropical trees, relative to the different architectural models. He found that the duration of the non-flowering stage and the degree of the first flowering branch-orders depended directly on the complexity of the tree´s architecture. The juvenile plant is incapable of flowering, but, from a specific grade of differentiation onwards, flower formation represents a normal morphogenetic stage. As regards the entire tree, sexuality shows an acropetal gradient which is negatively correlated with the decrease in vegetative vigour. In its extreme case, the flowering canopy of a modular tree for example may produce only miniaturized reiterations of the architectural model, flowering on all branches and exhibiting a more herbaceous than arborescent behaviour (see Hallé et al. 1978:277). Within a single individual the tendency to increase ontogenetic abbreviations with age is thus present. But, sexuality affects not only the canopy of an adult tree. As Barthélémy (1988) illustrated, in *Anaxagorea dolichocarpa*

(Annonaceae) the impulse to produce cauliflorous inflorescences may also progress basipetally, finally covering the entire shoot system including the main stem (fig. 226). Thus, the 'autocatalytic' expansion of sexuality is very complex and shows gradients in space and time.

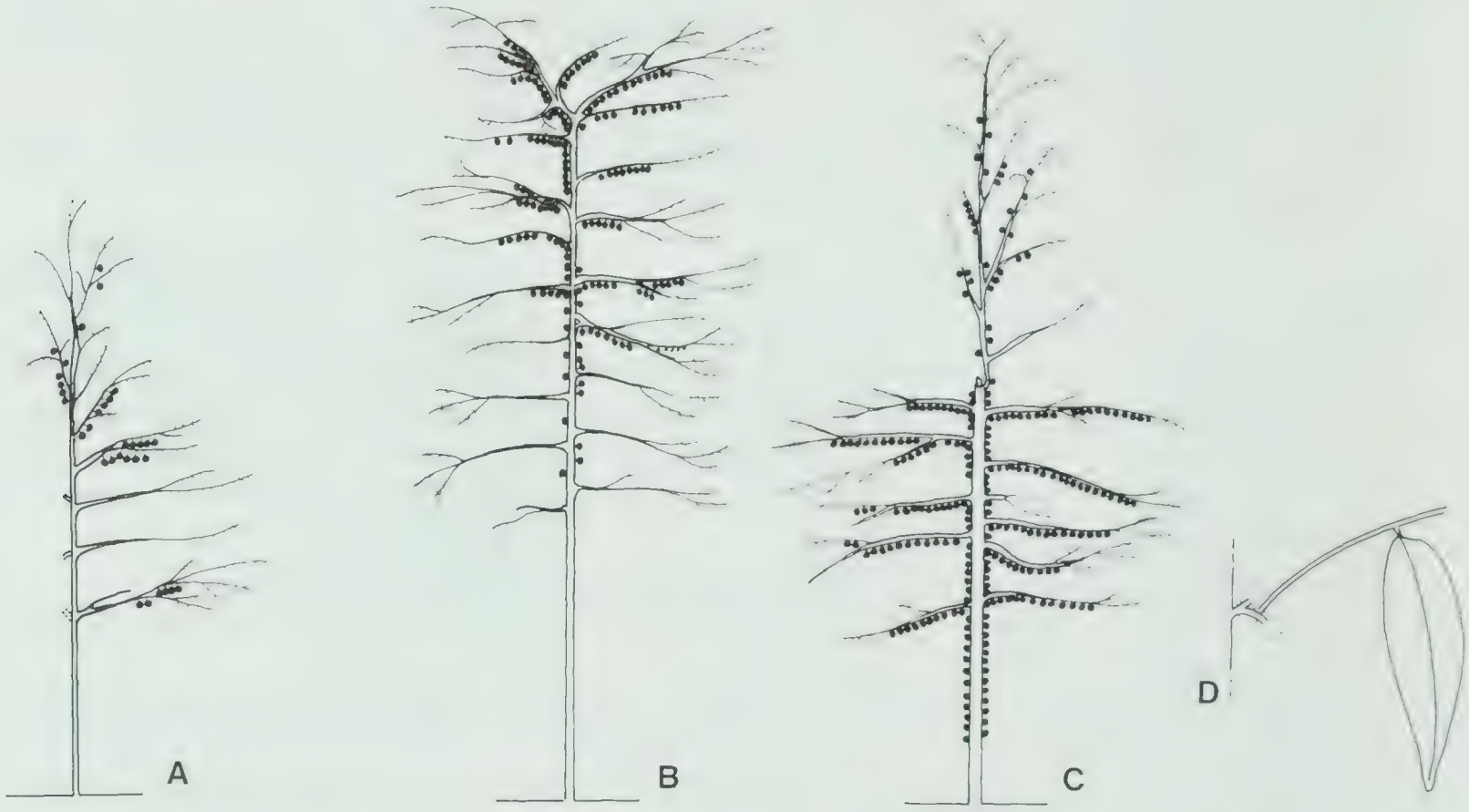


*Figure 226 - **Flowering behaviour in** **Anaxagorea dolichocarpa** **(Annonaceae)**. A, Young tree of about four metres in height starting to flower at lateral branches, B, tree of about six metres in height with cauliflorous inflorescences at both, lateral branches and main stem, C, very old tree completely sexualized down to its base. Note that sexuality increases with age (A-C) and that leafy shoots may arise from cauliflorous inflorescences in old trees (D). After Barthélémy1988.*

Gleißner (1998) associated the morphological method of growth form analysis with aspects of tree architecture. He interpreted the change in an ageing tree in space and time as a progressive variation of a single constructional unit, the 'Zuwachseinheit' (ZE) (formerly called 'organisational unit' by Froebe & Gleißner 1995). The ZE largely corresponded to the UE sensu Hallé et al. (1978), but was adapted to the specific conditions of temperate trees with e.g. definite internode curves, catalepsis, seasonal leaf loss and bud production (fig. 227). The reference system was related to the growth rhythm of the plant and not to the growth season, so that ZEs corresponded either to annual or to lammas shoots.

Following Gleißner (1998) the ZE is the elementary unit of (temperate) woody plants. Dependent on the quality of its apical meristem, the resulting shoot system shows a monopodial (A), sympodial (B,C) or mixed pattern. In the first case inflorescences appear only at lateral branches. The ZE concerned is 'heteromorphic' relative to the quality of its lateral meristems (A: vb, rb) either producing strictly reproductive shoots with no renewal capacity ('inflorescence shoots', A: is) or strictly vegetative shoots (A: vs). The same is found in 'ananthic-sympodial' shoot systems (B) in which the apical meristems of the individual ZEs become parenchymatous. Only 'anthetic-sympodial' shoot systems (C), which are characterized by a terminal flowering unit, show 'homomorphic' ZEs bearing only lateral meristems which repeat the meristematic pattern of their parent axis ('repeating shoots', C: rs).

Illustrating about twenty species of temperate trees in detail, Gleißner (1998) confirmed that the ZEs change with age in a characteristic manner. In young plants they are strictly vegetative showing an acropetal symmetry with the most prominant buds below the apex. When merging into the reproductive stage flowers were formed at formerly vegetative positions, thus being in competition either with the terminal bud, with proximal buds or with the distal renewal buds. In the latter case vegetative buds from the medial or even proximal part of the ZE have to renew the shoot system. With increasing age (1) the absolute length of the ZE decreases by shortening the internodes and by reducing their number, (2) the branching capacity decreases, (3) sympodial growth gradually increases because the apex merges into a flower or becomes parenchymatous, and, (4) most important, reproductive elements increasingly push

vegetative elements away finally producing strictly reproductive ZEs with no renewal capacity at all (compare with fig. 222, 223).

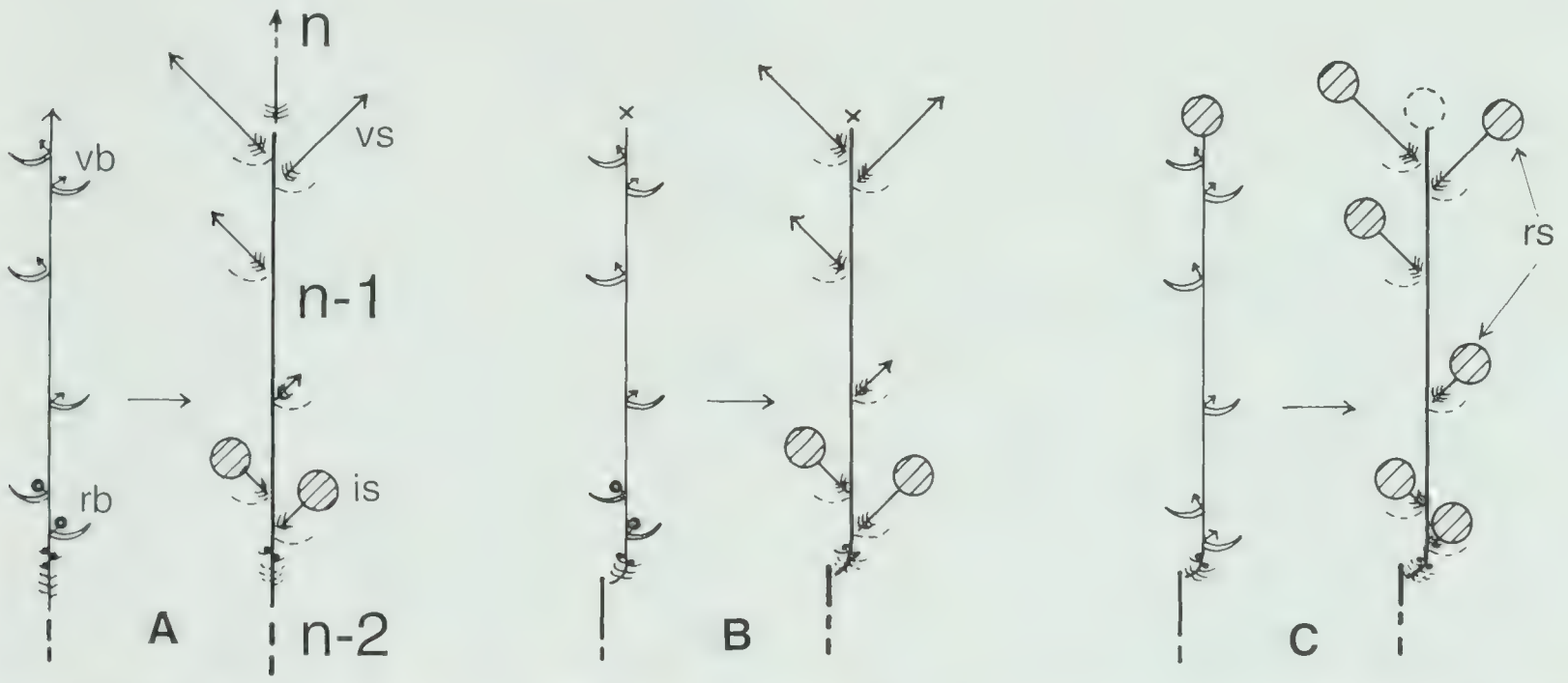


Figure 227 - ***The constructional unit `Zuwachseinheit' (ZE) and resulting branching patterns***. *The ZE corresponds largely to the UE sensu Hallé et al. (1978), but is adapted to the specific conditions of temperate trees showing (1) a rhythmic change in the length of the internodes, (2) a characteristic leaf metamorphosis and (3) a specific longitudinal symmetry, (4) time of development and (5) quality of the lateral meristems. A-C, examples of different types of ZEs all showing acrotony and catalepsis, but diverging in the quality of the apical meristem: A, ZE with a terminal bud causing monopodial shoot chains, B, ZE with an apex dying off causing an ananthic-sympodial branching pattern, C, ZE with terminal flower/inflorescence causing an anthetic-sympodial branching pattern. Note that the lateral meristems are heteromorphic in A and B and homomorphic in C.*

is, *inflorescence shoot,* rb, *reproductive bud,* rs, *repeating shoot,* vb, *vegetative bud,* vs, *vegetative shoot.*
After Gleißner (1998).

Gleißner (1998) discussed many aspects of tree architecture. With respect to the present investigation, the relative positions of inflorescences and renewal shoots is of special interest. Gleißner (1998) was able to show

- that, in *Castanea sativa* (fig. 228), the gradual reduction of the ZE from above results in a positional displacement of both the inflorescence, which becomes secondarily terminal (D), and the formerly terminal but lost renewal zone, which is substituted by vegetative shoots from the medial part of the ZE (E);
- that, in *Betula pendula* (fig. 229), renewal capacity may be transferred to a reproductive short-shoot after complete reduction of the upper part of the ZE (C-E: rz);
- that, in *Tilia cordata* (fig. 230), the sylleptic reproductive short-shoots regularly bear renewal buds (rz').

Though the latter two species both show renewal capacity at reproductive short-shoots, Gleißner (1998) interpreted the positional displacements in a different manner. As *Betula pendula* shows an anthetic-sympodial branching pattern, homomorphic lateral meristems were expected. For that reason Gleißner interpreted the reproductive short-shoots as neotenic ZEs. In contrast, *Tilia cordata* follows the ananthic-sympodial branching pattern in having heteromorphic lateral meristems. For that reason the reproductive short-shoots were neither strictly reproductive 'inflorescence shoots' nor neotenic ZEs. As the number of renewal buds is limited in ananthic shoot systems, Gleißner (1998) concluded that renewal capacity had shifted from the vegetative ZE onto the reproductive ZE in order to increase the chance of renewal after the heavy shortening of the ZE and loss of vegetative buds.

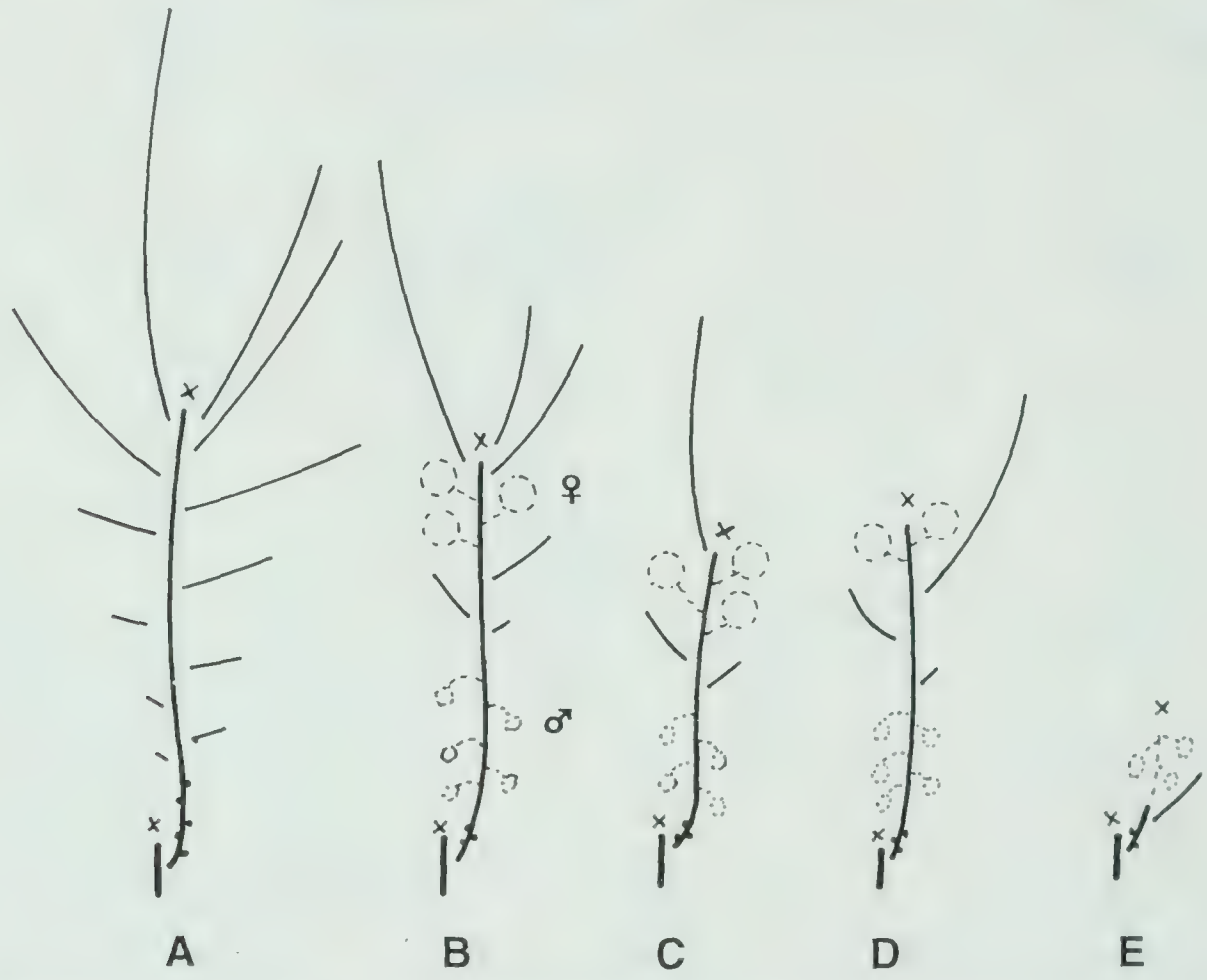


*Figure 228 - **Metamorphosis of the ZE in* Castanea sativa.** *A, vegetative stage characterized by acrotony and catalepsis, B-D, adult stages with sylleptic inflorescence shoots (proximal: male; distal: female) and an increasing tendency to reduce the ZE from above; in D the subterminal renewal zone is completely lacking and vegetative buds below the secondarily terminal inflorescence function as compensation. E, senescent stage: the ZE is heavily reduced from above, bearing only male inflorescences and latent buds which are nevertheless capable of taking over the function of renewal. After Gleißner (1998) (who cited Drénou 1994 in E).*

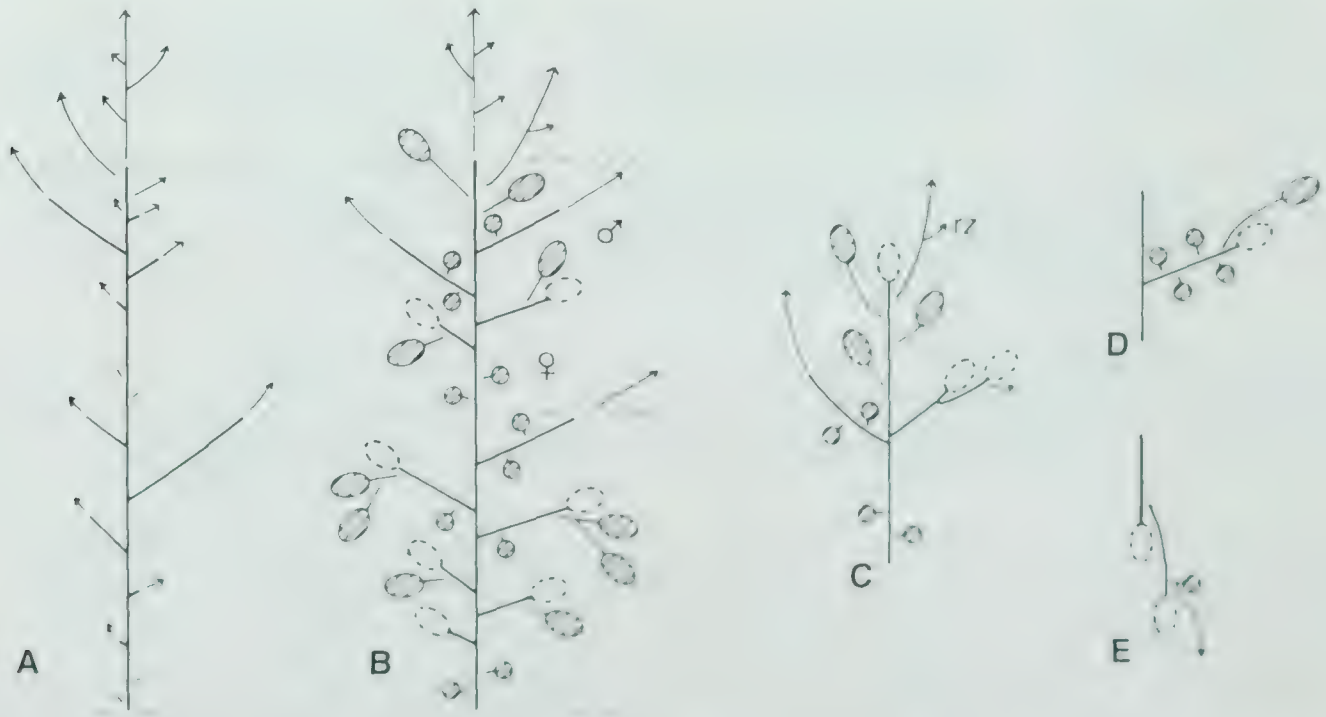


*Figure 229 - **Metamorphosis of the ZE in* Betula pendula.** A,B, *extended ZEs of the vegetative (A) and early adult stage (B) being characterized by an increased number of nodes, sylleptic lateral and lammas shoots. Note that the female short-shoots in B are found at the basal position of the vegetative short-shoots in A, and that the most prominant lateral shoots in B end in a terminal bud while all remaining shoots terminate in a male inflorescence. C, typical ZE of the reproductive stage with terminal male inflorescence and proximal female short-shoots. The acro-mesotonous symmetry is the result of two superimposed gradients. D, E, reduced ZEs in plagio- and geotropous positions showing the lack of the entire sylleptic part of the ZE in D, and the additional lost of the apical zone in E; the renewal shoot in E arises from the female short-shoot which is interpreted to be a neotenous ZE. After Gleißner (1998)*

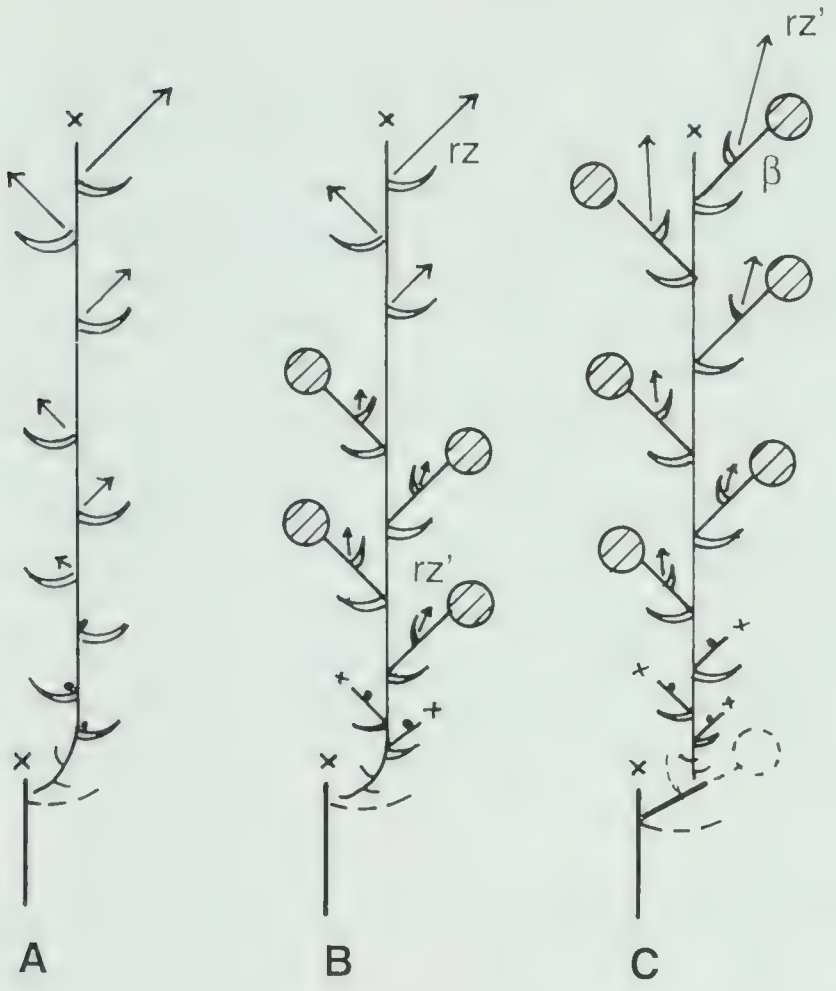


*Figure 230 - **Metamorphosis of the ZE in* Tilia cordata**. A, vegetative stage showing the ananthic-sympodial branching pattern, B, early adult stage with renewal buds in the distal part of the ZE and additional renewal buds in the ß-prophylls of the sylleptic lateral flowering shoots, C, adult stage showing the complete reduction of the subterminal renewal zone and its compensation by the left buds in the ß-prophylls of the lateral flowering shoots.*

After Gleißner (1998).

4.2.5 Summary

The historical survey on concepts and disputes in inflorescence morphology has illustrated that the two basic questions at the beginning of § 4 were answered quite differently during the past decades. Dependent on the individual point of view typological, morphogenetic, strictly descriptive and dynamic approaches were made each introducing its own terminology and reference framework (fig. 231, tab.1).

With regard to inflorescences of woody plants two main disciplines have evolved in the 20th century: inflorescence and growth form morphology. Parkin (1914) and Pilger (1922) may represent the early beginnings of the two different views. While the first analysed the structure of inflorescences, the latter analysed flowering 'pushs' and thus entire woody shoot systems bearing inflorescences. Dominated by the outstanding morphologist Troll both disciplines were largely influenced by his typological view. As to the concept of synflorescences the pros were the identification of identical structures independent of habit and foliage and the resulting chance to homologize inflorescences of different species while the cons were the circumscription of the introduced types, the interpretation of 'proliferating synflorescences' and the use of 'flowering innovation shoots' as references for the delimitation of synflorescences in woody plants. Besides the concept of Troll a physiologically influenced view evolved in France (see Maresquelle 1977) resulting in dynamic approaches of both inflorescence morphology (e.g. Sell 1976) and tree architecture (e.g. Hallé et al. 1978). A strictly descriptive approach which nowadays is well known in English speaking countries was introduced by Briggs & Johnson (1979) for systematic purposes.

Troll's typology was criticized from the beginning resulting in alternative definitions of inflorescences and their delimitations in woody plants.

- Kunze (1989) argued that because of evolutionary repetitions the presentation of only two types would be unacceptable. Schröder (1987) and Kusnetzova (1988) consequently restricted the term synflorescence to a pattern that will be repeated on different levels of organization.
- The application of the term synflorescence to an entire flowering innovation shoot in perennial and woody plants resulted in manifold problems. Some of them were the high number of 'proliferating synflorescences' (§ 4.2.3.2), the appearance of synflorescences several seasons of age (Endress 1970, Jager 1980) and of those which were not at all composed of florescences (Bayer 1994). While the authors cited tried to keep to the dominant concept, Van Steenis (1963) and Schröder (1987)

rejected it defining the `inflorescence´ as a strictly reproductive ephemeral shoot system bearing flowers.

- As Parkin (1914) and Pilger (1922) before them, Briggs & Johnson (1979) and Sell (1982) pointed out the analogy between indeterminate inflorescences in woody plants which may have evolved either from a terminal inflorescence by truncation or from an indeterminate woody shoot system by aggregation of its laterally arranged flowers/inflorescences and inhibition of the activity of the apical meristem. Sell (1982) showed that both levels of complexity, the caducous inflorescence and the persistent flowering shoot system might be regulated by the same elementary physiological processes (e.g. homogenization) resulting in similar but analogous patterns.
- Studies on the growth form morphology of woody plants illustrated that the position, sex and time of development of individual inflorescences were largely influenced by the polarity of the shoot system and the vegetative vigour of the shoots (Hauser 1932, Schützsack 1965). Studies on tree architecture clearly showed that the latter decreases with age in favor of an increasing sexuality. The entire tree passes through a metamorphosis during lifetime characterized by increasing neoteny which is reflected in manifold reductions and miniaturizations of the underlying architectural model (Hallé et al. 1978, Barthélémy 1988). As a result of `terminalization´ inflorescences may appear laterally in young and terminally in older plants (Hamann 1960) and renewal zones may be present or lacking dependent on the age of the plant (Gleißner 1998).

Concerning the problem of finding an appropriate reference system tab. 1 summarizes the reference units used by the individual authors. Despite their different names they refer to three different growth cycles only:

(1) The cycle of organization reflects the time-independent developmental programme of a shoot system which is either sympodial or monopodial (or mixed). The corresponding terms mainly characterize sympodial units which usually are easy to recognize and, in contrast to monopodial units, may differ from the units of extension.

(2) The cycle of extension reflects the time-dependent growth rhythm of a shoot system which appears seasonally but also reflects endogenous parameters. The terms `Schub´ and `Zuwachseinheit´ in particular point to the possible appearance of lammas shoots each being an individual unit and not part of a superior cycle of extension (Pilger 1922, Gleißner 1998).

(3) The cycle of initiation is represented by the unit of morphogenesis. It is a unit of time but independent of seasons or other external influences, thus being intermediate between the cycle of organization and the cycle of extension.

*Table 1 - **Reference units** used by individual authors.*

term	author	reference
`article´ `module´ two season old shoot system multiseasonal paraclade s.l. sympodial/monopodial unit	Prévost 1967 Hallé et al. 1978 Endress 1970 Jäger 1980 Bell 1991	cycle of organisation
morphogenetic stage `unit of morphogenesis´ (UM)	Schützsack (1965) Hallé et al. (1978)	cycle of initiation
Schub `blühender Innovationstrieb´ physiological stage `unit of extension´ (UE) `seasonal growth unit´ (SGU) `Zuwachseinheit´ (ZE)	Pilger 1922 Troll (e.g. 1964) Schützsack (1965) Hallé et al. (1978) Briggs & Johnson (1979) Gleißner (1998)	cycle of extension

developmental programme

growth rhythm

As the studies cited show both the cycle of organization and the cycle of extension appear to be equally useful for scientific research and merely reflect different views relative to flowering woody shoot systems. The unit of extension appears to be adequate to growth form morphology and studies on tree architecture while the unit of organization may be preferred by inflorescence morphologists (see 4.3.2).

Concerning the problem of finding the reproductive unit fig. 231 summarizes that inflorescences were either defined as physiological (Van Steenis 1963, Schröder 1987, Sell & Cremers 1994) or as structural units (Troll 1964, Briggs & Johnson 1979). The first are caducous by definition and thus easy to separate from the prospective woody part of the shoot system, while the latter largely correspond to flowering patterns which may or may not superimpose vegetative structures.

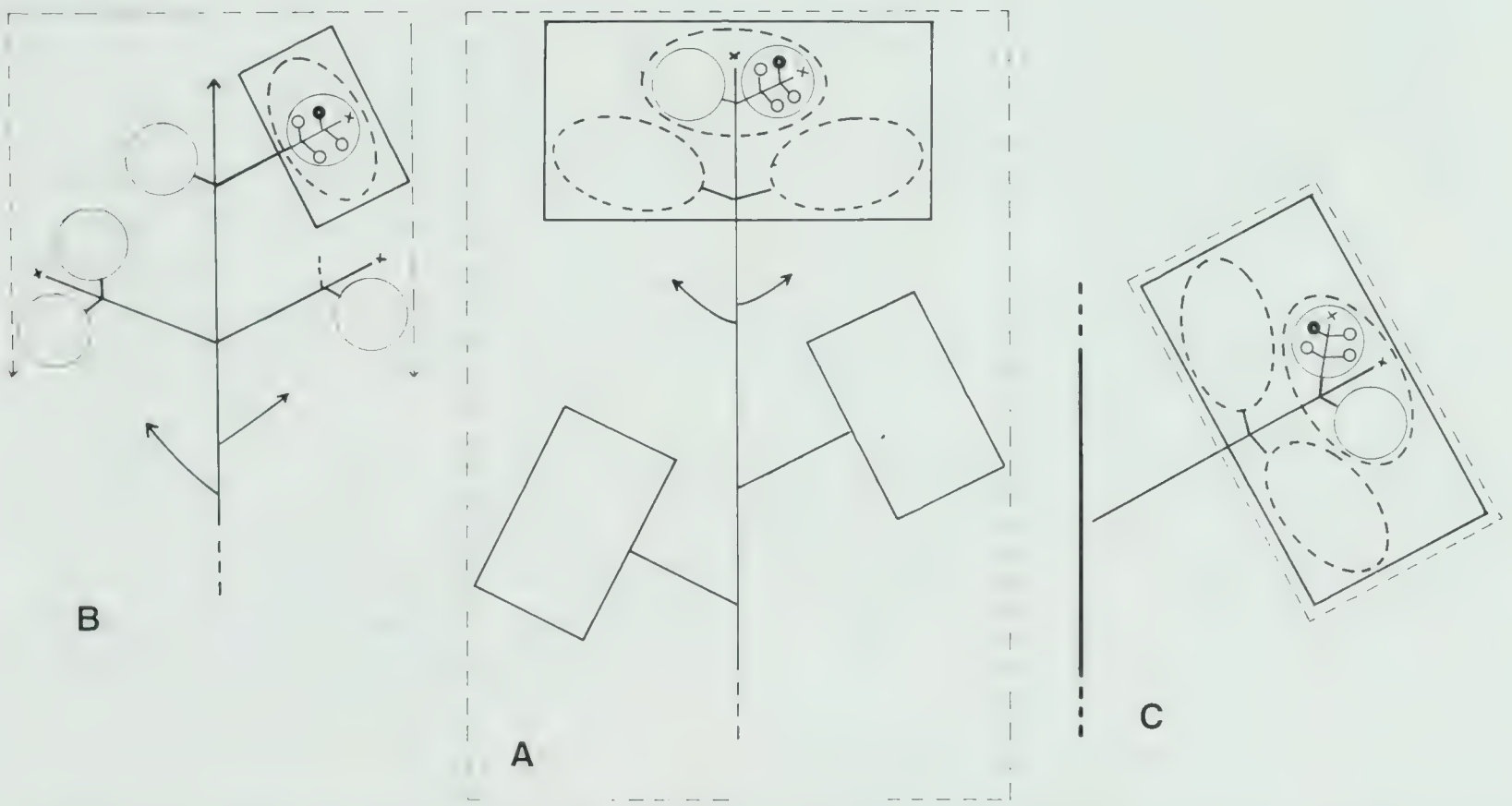


*Figure 231 - **Characterization of flowering units**. A, illustration of the different terms used in literature. B,C, the units described by the individual terms change with the perennial nature of the main axis (B) and the cataleptic development of the lateral shoots (C). Black: uniflorescence (U) sensu Briggs & Johnson (1979), circle: polytelic florescence (F) sensu Troll (1964), dotted circle: unité de floraison (UF) sensu Sell & Cremers (1994), frame: inflorescence sensu Van Steens (1963) and Schröder (1987) = synflorescence s.str. (p. 251), dotted frame: synflorescence s.l. (p.251).*

4.3 The `brunioid´ reference framework

As shown in the previous chapter it is necessary in woody plants to distinguish between two levels of complexity, the level of the growth form and branching pattern of the entire plant and the level of the inflorescences. The first deals with the relative position of both the renewal zones and the inflorescences, with the delimitation of individual inflorescences within the woody plant body and with the changes of the plant´s architecture with age. The second in contrast deals with the structure of a delimitated inflorescence and with the relative position of parts within this unit.

4.3.1 The architecture of Bruniaceae

All Bruniaceae grow as shrubs ranging from prostrate rock crevice species up to tree-like plants of four meters in height. They are characterized by sympodial shoot systems, which age less than one season, one season or more than one season (fig. 232). Usually the individual SGU is sylleptically branched and often shows mesotony in erect and hypotony/epitony in prostrate shrubs. The main renewal zone appears below the terminal flower/inflorescence in determinate and below the apex in indeterminate shoot systems. It may be lacking in case of a dominant shoot which continues to grow on. As regards the activity of the apical meristem of the dominant shoot of an individual SGU three groups are distinguishable.

(1) *Staavia* (except *S. verticillata*) and *Lonchostoma* (except *L. esterhuyseniae*) always show a terminal inflorescence, thus representing the anthetic-sympodial type with homomorphic lateral shoots (see § 4.2.4.2).

(2) *Audouinia, Linconia, Pseudobaeckea teres, Tittmannia* and *Berzelia* in contrast never form a terminal flower/inflorescence (ananthic-sympodial type) and for that reason always bear heteromorphic lateral shoots (vegetative and inflorescence shoots). However, regarding the shoots of the 1st order of branching, *B. abrotanoides, B. galpinii* and *B. ecklonii* show a `flexible condition´ (sensu Briggs & Johnson 1979) bearing both determinate and indeterminate lateral shoots. They therefore lead over to the next group

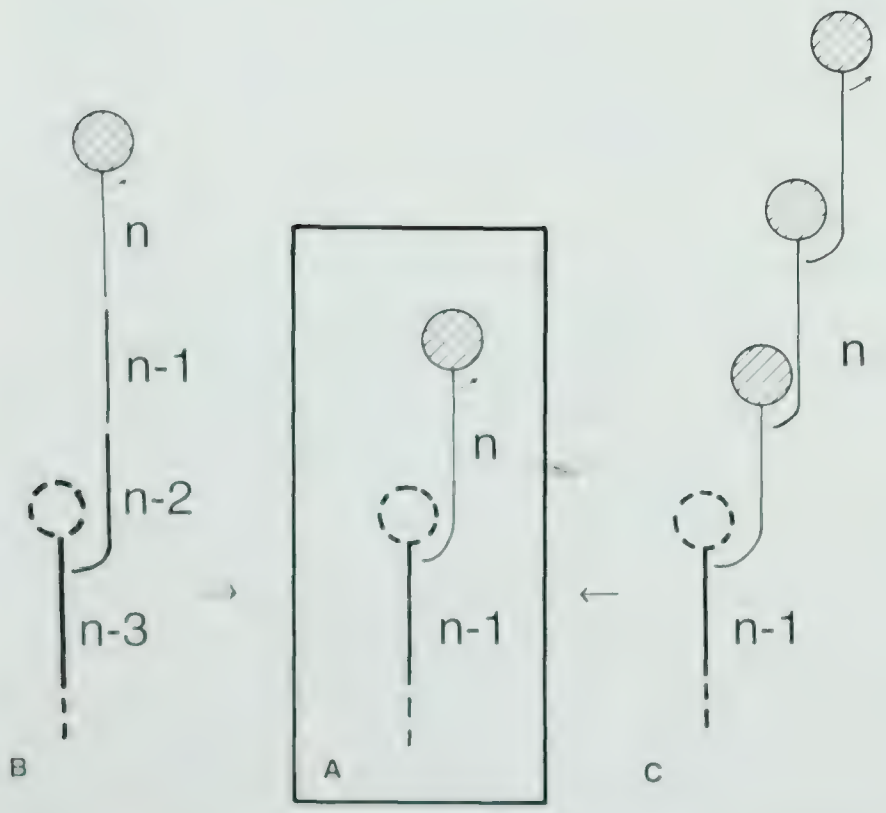


*Figure 232 - **Complementary correlation between the unit of organisation (SU) and the unit of time (SGU).** A, flowering shoot system that coincides at the same time with one SU and with one SGU. B, C, shoot systems illustrating extreme differences between the SU and the SGU.*

(compare with fig. 203)

(3) comprising the remaining genera. The latter either comprise species of both groups (1) and (2) (e.g. *Brunia macrocephala, Brunia alopecuroides*) or species which only facultatively form a terminal flower/inflorescence at the top of the main shoot (e.g. *Brunia nodiflora*), in this way demonstrating the flexible condition of the apical meristem. In the latter case it is often found, that the dominant shoots are capable to grow on for several seasons (monopodial shoot connections) before merging

into a terminal flower/inflorescence, while the lateral shoots terminate much earlier in a flower/inflorescence and then renew sympodially. The lateral (homomorphic) shoots thus repeat the branching pattern of the dominant shoot in an abbreviated manner.

In accordance with Hallé et al. (1978) and Gleißner (1998) it could be shown in many species of Bruniaceae (e.g. *Nebelia fragarioides*, fig. 117) that the vegetative vigour of the plants decreases with age. The most striking changes are the gradual decrease of the length and branching capacity of the SGU and the change of monopodial to sympodial shoot connections. Fig. 233 summarizes the life cycle of the Bruniaceae in a highly generalized manner. However, as the early stages of prostrate plants are not known the scheme predominantly refers to erect species:

(1) The juvenile stage (A, B) is characterized by a powerful orthotropic growth (fig. 16, 101). The vegetative body is formed by branched long-shoots which are similar to each other in the beginning, but become gradually more different with age. The primary shoot (P) either continues to grow on for several seasons producing monopodial units (B, e.g. *Staavia dodii*: 5-8 years, see Moll & Gubb 1981) or dies off at the end of the present season (A, e.g. *Nebelia fragarioides*, fig. 101). According to Hallé et al. (1978: 151-153) endogenous and exogenous stimuli may cause the parenchymatous condition of the apical meristem.

(2) The transitional stage (C,C′) between the strictly vegetative youth (A, B) and the flowering adult stage (D-E′) is characterized by the gradual decrease of the vegetative vitality of the plant. Dependent on the ananthic- (C) or anthetic-sympodial mode (C′) two different branching patterns result. In case of the latter (C′) all shoots are homomorphic 'repeating shoots' (rs) being able to flower and to produce renewal shoots at the same time. However, as the lateral shoots are weaker than the dominant ones sexuality covers them first. They usually terminate in a flower/inflorescence and continue in a sympodial manner (e.g. *Raspalia variabilis*, fig. 151). They may be branched and retain the capacity to renew part of the shoot system (e.g. *Staavia glutinosa*, fig. 166: rz′) or they are highly abbreviated compared with the dominant shoot. The latter grows on for several seasons in a monopodial manner before merging into a terminal flower/inflorescence, thus completing the sympodial cycle. With regards to the ananthic SUs (C) it is clear by definition that sexuality always and only covers lateral shoots. In contrast to the anthetic mode these inflorescence shoots (is) never bear renewal shoots (e.g. *Berzelia*, § 3.2). The leader shoot usually grows on for several seasons before the apex becomes exhausted and dies off. Independent of the ananthic or anthetic type, the monopodially connected flowering SGUs often appear as 'proliferating' inflorescences (e.g. *Audouinia capitata*, fig. 11). Referring to the zoological concept of neoteny where juvenile stages already become fertilized, the transitional stage may be called the 'pubescent' stage of the plant. It is characterized by a vegetatively dominated leader shoot and already sexualized lateral shoots.

(3) The fully adult stage (D-E′) is characterized by a decreased branching capacity and an increased sexuality. The length of the individual SGUs gradually decreases with age (e.g. *Staavia glutinosa*, fig. 164) and, particularly in case of anthetic SUs, a regular sympodial branching pattern is established (D′). In the extreme case, no renewal capacity at all is found in the flowering SGUs (E, e.g. *Nebelia laevis*, fig. 111A, E′, e.g. *Nebelia fragarioides*, fig. 105). The shoot system then is characterized by a structural SGU-dimorphism and a functional division of labour. In general the architecture of the adult plant is characterized by much branched lateral systems, occasionally forming a 'canopy', and a less branched orthotropic or plagiotropic 'stem' (e.g. *Berzelia galpinii*, fig.42C, *Raspalia microphylla*, fig. 150). In anthetic-sympodial shoot systems the transitional (or pubescent) stage (C′) may be omitted as shown by *Staavia dodii*, where the sympodially branched reproductive stage (D′) abruptly follows the monopodially organized vegetative stage (B). Ananthic shoot systems in contrast tend to leave out the stage of regular sympodial branching (D), the entire adult stage then being represented by the so-called pubescent stage (C). Despite the high symmetry in adult plants differences from the regular pattern are not only possible, but necessary for the rejuvenation of the plant. Strictly vegetative SGUs appear as well as vigorous lateral shoots which grow on vegetatively for several seasons ('Schosser', 'juvenile reiteration', see Pilger 1922:10, Troll 1937:651, Rauh 1939:105, Hallé et al. 1978:16, 175, Hagemann 1989: fig. 6). In like manner sprouting from old wood rejuvenates the plant after fire (e.g. *Berzelia abrotanoides*, fig. 36C, 38).

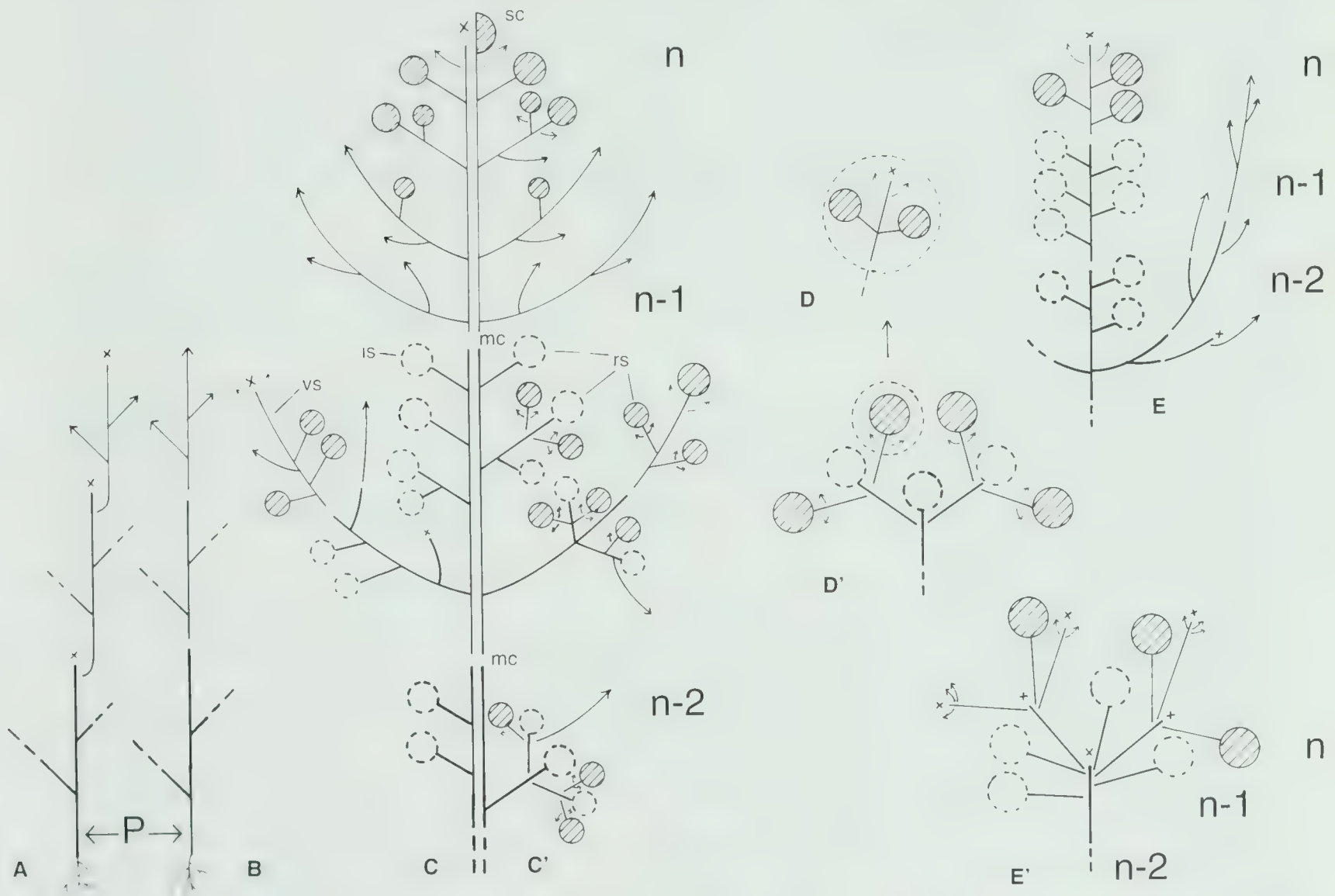


Figure 233 - ***Generalized scheme of the life cycle in Bruniaceae****. A,B, juvenile stages showing sympodial (A) and monopodial (B) connection of the first SGUs, C,C´, transitional (or pubescent) stage illustrating a several seasons old SU bearing monopodial inserts; in case of ananthic SUs (C) the lateral shoots are heteromorphic either being strictly vegetative (vs) or strictly reproductive (is), while in case of anthetic SUs (C´) the lateral shoots repeat the dominant shoot in an abbreviated manner (rs). D,D´, adult stages of plants characterized by a regular sympodial branching pattern (D only rarely realized in Bruniaceae), E,E´, adult stages being characterised by a division of labour caused by SGU-dimorphism.*

is, *inflorescence shoot,* P, *primary axis,* rs, *repeating shoot,* vs, *vegetative shoot.*

4.3.2 The `brunioid´ reference system

In Bruniaceae the SUs vary in time. To eliminate this variation the reference system (RS) represents the singular case that one SU exactly coincides with one SGU (fig. 232A). As both, the unit of organization and the unit of time, appear as equivalent units, complementary statements are possible: one SU may be part of one SGU (fig. 232C, e.g. *Lonchostoma myrtoides*, fig. 84A), may correspond to one SGU (fig. 232A, e.g. *Raspalia staavioides*, fig. 137) or may age more than one SGU (fig. 232B, e.g. *Muothamnea bullata*, fig. 92A). And: one SGU may produce the part of one SU (B), may correspond to one SU (A) or may comprise more than one SU (C). The practical advantage of this procedure was illustrated in the highly diverse shoot systems of Bruniaceae where alternatively either the SU or the SGU were analysed first (see fig. 203). In a second step the complementary unit was added. By doing so the difficulties were largely eliminated which always appeared when the SU and the SGU did not coincide or when no clear limits between succeeding SGUs were found. As a useful result a model for each genus could be presented which simplified the comparison between the individual genera (see §3).

The RS applied to the Bruniaceae (fig. 234) refers to the characters of the family. It represents a one season old SU which either shows an ananthic (left side) or an anthetic organization (right side). It is subdivided from proximal to distal into the insertion- (rz-1), branching- (bz), renewal- (rz) and apical zone (az). The insertion zone coincides with the renewal zone of the parent shoot, the branching zone is defined as bearing sylleptic vegetative and flowering lateral shoots, the renewal zone as bearing the

primordia of the cataleptic renewal shoots and the apical zone as merging into a terminal flower/inflorescence or as dying off.

Compared with the generalized life cycle (fig. 233) the RS summarizes to a large extent the characters of the transitional stage which is the most complete and variable one bearing vegetative and reproductive elements at the same time. In this circumscription the RS represents a central pattern to which the highly diverse individual patterns of flowering shoot systems in Bruniaceae are referable. It does not include any phylogenetic informations or represent any primitive or derived states.

4.3.2.1 Plasticity of the reference system in Bruniaceae. Compared with the RS the individual plants show numerous differences covering quantitative and qualitative variants as well as changes in symmetry, habit and time.

- The apical zone (fig. 234: az) comprises the apex of the main axis which, dependent on the underlying type, dies off (ananthic) or merges into a terminal flower or (in)determinate inflorescence at the end of the season (anthetic). It is always referred to the top of the SU and must not be mixed up with the distal part of a SGU. Only the latter may have an active apical meristem growing on for the next season.
- The renewal zone (fig. 234: rz) bears the renewal shoots which usually develop cataleptically. In Bruniaceae, however, the renewal shoots often start to grow on sylleptically remaining vegetative (e.g. *Raspalia globosa*, fig. 134B) or already merge into floral bud production (e.g. *Brunia nodiflora*, fig. 53, *Tittmannia esterhuyseniae*, fig. 191D, 194) before passing a dormant stage. In the extreme case sylleptical SUs are formed which flower, fruit and produce renewal zones like the parent axis (e.g. *Staavia dregeana*, fig. 171: sfR).

  Dependent on the growth form of the plant the individual renewal shoots are equal or unequal in length. Particularly in prostrate shrubs, hypotony and epitony play an important role (e.g. *Mniothamnea bullata*, fig. 92A, *Pseudobaeckea teres*, fig. 129, *Raspalia microphylla*, fig 150, *Thamnea massoniana*, fig. 183). But also in erect shrubs the unequal length of the renewal shoots resulting in few long and many short shoots may effectively influence the architecture of the plants (e.g. *Raspalia virgata*, fig. 142, *Tittmannia laxa*, fig. 197).

  The number of renewal shoots per renewal zone varies from one up to ten or more (e.g. *Tittmannia laxa*, fig. 198A), but usually ranges around four in Bruniaceae.

  Dependent on the degree of branching and flowering a strict delimitation between renewal zone and branching zone may be lacking resulting in a mixture of flowering and renewal shoots (e.g. *Nebelia sphaerocephala*, fig. 108) or in 'flowering' renewal shoots where the apex of indeterminate lateral shoots renews the shoot system (e.g. *Berzelia galpinii*, fig. 45: R, *Brunia albiflora*, fig. 66E). Rarely the renewal zone is lacking completely being substituted by the renewal zones of the repeating shoots (e.g. *Brunia albiflora*, fig. 66D, *Raspalia virgata*, fig. 142: rz'). The example of *Staavia glutinosa* (fig. 164B: n) illustrates that the vegetative vigour of the entire SU may be reduced to a few renewal zones of 1st order leading over to strictly reproductive units (fig. 233E').

  As regards renewal capacities in general (1) sylleptic vegetative lateral shoots from the branching zone often function as additional (e.g. *Nebelia sphaerocephala*, fig. 109A: me) or even only renewal shoots. In the latter case these shoots may resemble renewal shoots arranged below a compound inflorescence and only a detailed analysis of several shoot systems elucidates that they in fact originate from the branching zone (e.g. *Brunia albiflora*, fig. 66, *Brunia*, fig. 76A-C). (2) Additional renewal capacities are also preserved by lateral shoots produced in preceding seasons (e.g. *Nebelia paleacea*, fig. 114). These 'late' renewal shoots usually originate from the branching zone of the SGU concerned and thus are referable to the RS. (3) In contrast to the definition of the RS, individual SUs may age several seasons. The apical meristem of individual SGUs then continue to grow on in the next season often representing the only vegetative meristem of the SGU concerned (fig. 233E: n-1).
- The branching zone (fig. 234: bz) usually represents the largest and most variable part of the RS. It may be branched (e.g. *Raspalia microphylla*, fig. 150) or unbranched (*Staavia glutinosa*, fig. 202A), strictly vegetative (e.g. *Nebelia fragarioides*, fig. 102) or reproductive (e.g. *Berzelia incurva*, fig. 34), or characterized by both vegetative and flowering lateral shoots. In the latter case the branching zone may be subdivided into a distal flowering and proximal vegetative zone (e.g.

Brunia alopecuroides, fig. 72), or both kinds of lateral shoots are arranged in a mixed pattern. The lateral shoots may develop sylleptically or (late) cataleptically. They are branched or unbranched and, in case of flowering, determinate or indeterminate. They do or do not have a renewal capacity of their own.

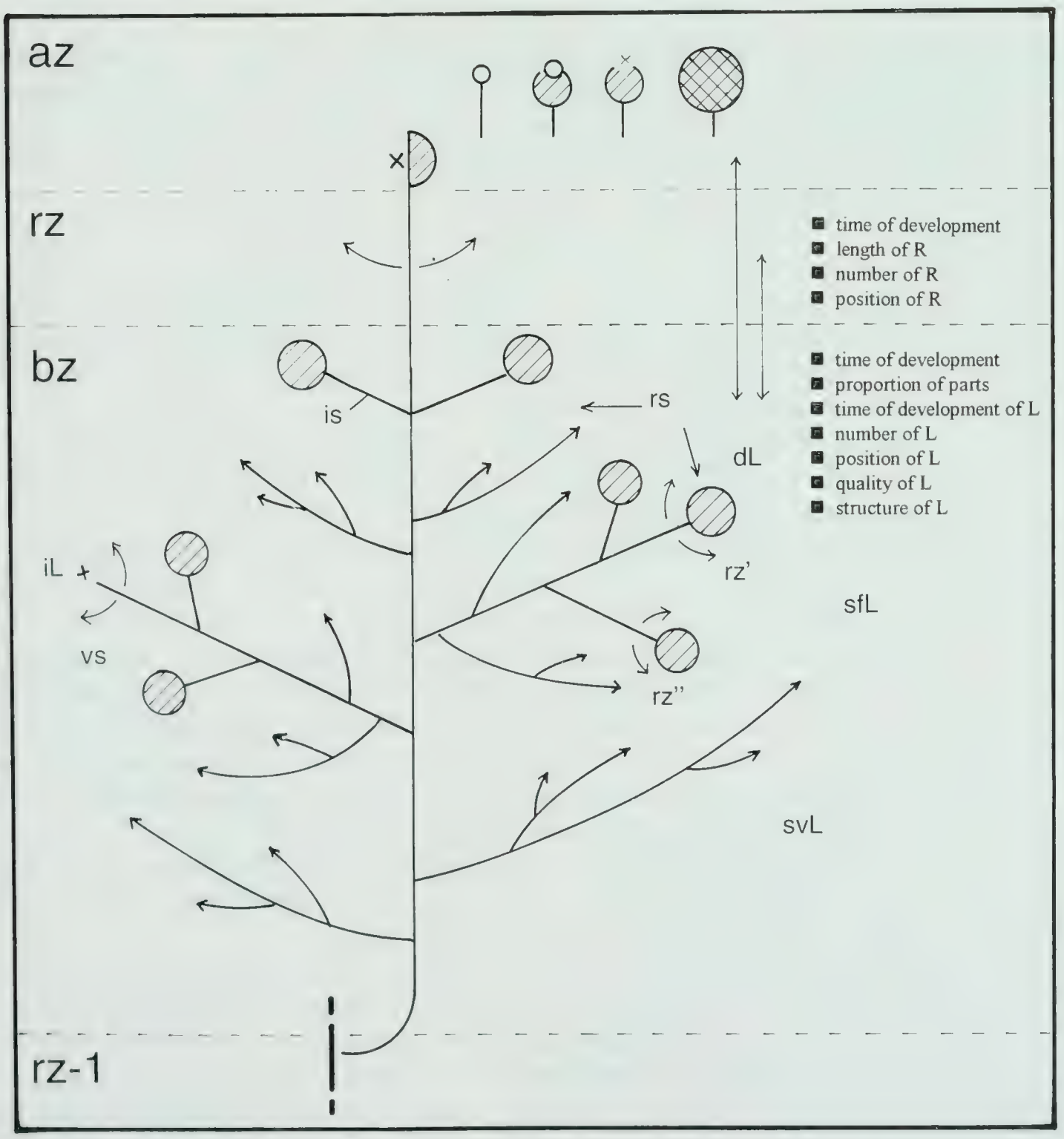


*Figure 234 - **The reference system applied to the Bruniaceae**. The RS is defined as a flowering, prospectively woody shoot system that coincides at the same time with one SGU and one SU. It comprises the apical zone (az), which dies off (ananthic mode; left) or bears the terminal flower/inflorescence (anthetic mode; right), the renewal zone (rz) with the primordia of the usually cataleptic renewal shoots, the branching zone (bz) bearing sylleptic vegetative and flowering lateral shoots and the insertion zone (rz-1). The characterization of the individual zones illustrates the typical or maximal equipment of each and is largely referred to the transitional stage of the generalized life cycle (fig. 233C,C'). The variants added show that the RS represents only one of the numerous character combinations. It thus represents a central pattern to which all individual cases may be referred and includes no phylogenetic information.*

is, *inflorescence shoot*, rs, *repeating shoot*, vs, *vegetative shoot*.
Arrows: interactions between different zones, black bullets: variable characters within one zone.

The arrangement of the sylleptic flowering lateral shoots may directly influence the size and individuality of what is called an inflorescence. In *Audouinia capitata* for example 'proliferating spikes' appear which, however, are arranged below the renewal zone and thus interpreted as aggregates of uniflorous short-shoots originating from the branching zone (fig. 8A). In *Pseudobaeckea africana* (fig. 126) compound inflorescences appear which are composed of the

terminal inflorescence of the apical zone and the uppermost sylleptic flowering lateral shoots of the branching zone. The extreme form is realized in *Staavia zeyheri* (fig. 174B) where the uppermost lateral cephaloids are densely aggregated near the top of the SU pretending a compound inflorescence similar to that of *Nebelia fragarioides* (fig. 101B), but in fact only hiding the cataleptic renewal shoots which arise below the terminal cephaloid.

4.3.2.2 The reference system tested against other plant groups. The reference system presented is the result of empirical studies in the Bruniaceae (§ 3). It differs from all existing systems in combining the two complementary aspects of organization (SU) and time (SGU) to a single reference system. In doing so it was possible to subdivide the RS into zones which renders the clear comparison between different shoot systems and species possible.

Though the system was originally established for the Bruniaceae it may be valuable for other plant groups, too, particularly for those which resemble Bruniaceae with respect to their syllepticaly branched woody shoot systems (e.g. many Myrtaceae, Ericaceae, Asteraceae, Proteaceae). The application to woody plants of different growth behaviour or of temperate climates is much more difficult, but appears to be principally possible.

- In the Hamamelidaceae *Parrotia* and *Distylium*, the units called synflorescences by Endress (1970) (fig. 215: thick lines) are both referable to a syllepticaly branched RS because the latter eliminates the differences in the time of development by definition.
- The Betulaceae (see Hauser 1932: fig. 222; Jäger 1980: fig. 216; Gleißner 1998: fig. 229) represent a highly derived group showing (1) sex dimorphism, (2) the combination of sylleptic and cataleptic development each connected with a specific longitudinal symmetry (e.g. fig. 222), (3) the presence of an extreme long-shoot short-shoot dimorphism including miniaturized models (laterally arranged male catkins) and monopodial inserts (e.g. fig. 216B), as well as (4) the multiple positions of the renewal shoots which appear likewise at the main axis and at lateral flowering shoots (e.g. fig. 216C, 229D,E). However, as Jäger (1980) and Gleißner (1998) have illustrated all shoot systems (`synflorescences´ sensu Jäger, `Zuwachseinheiten´ sensu Gleißner) are derivable from a starting-form and therefore also referable to an anthetic, syllepticaly branched RS.
- Replying to the critical comments of Sell (1995) the same is true for shoot systems which are characterized by long-shoot short-shoot dimorphism or by cauliflory which are both taken as superior organizational units irrespective of the time of development.
- The objections to inflorescence morphology of Hallé et al. (1978) become largely irrelevant because inflorescences are not defined by their absolute position and time of development, but by their relative position and strictly caducous nature. However, it is necessary to analyse extended shoot systems to identify the reproductive unit of the species concerned.
- Applying the RS to monopodially branched plant groups (e.g. palms) the following more general definition is advisable: The RS represents a flowering, prospectively woody shoot system that at the same time coincides with one `cycle of extension´ and one `cycle of organization´ (tab. 1). In sympodial groups it corresponds to a one season old sympodial unit, while in monopodial groups it corresponds to a one season old monopodial unit. In the latter case it is largely identical to an individual SGU and thus the application of the RS to those groups makes perhaps less sense.

The present study proceeded from inflorescence morphology. Since in woody plants inflorescences are part of extended shoot systems some general remarks on the plants` architecture have become necessary. In search of an appropriate reference framework the `bruniod´ RS was introduced, not to substitute any constructional unit of growth form morphology but to be used as a central pattern for comparison. The short comments given above show that the presented RS is not exclusively made for the small and relatively unknown group of Bruniaceae, but might be a fruitful base for further discussions and attempted applications. The most important use of the RS, however, is the delimitation of the inflorescences and thus its contribution to inflorescence morphology (§ 4.3.3).

4.3.3 Reproductive units

The `brunioid´ reference framework comprises both levels of complexity, the level of the entire flowering shoot system (reference system) and the level of the strictly reproductive inflorescences (reproductive units). Returning to § 4.1.3 and the question of homology it appears appropriate to define the reproductive unit (RU) by its special reproductive quality (fig. 204E: 3).

Following Troll in interpreting all flowers of an innovation shoot as members of a superior synflorescence, a unit of time (fig. 204E: 1) is taken as reference. But, in view of the criticism summarized in § 4.2.3.2 and of the results of architectural studies, it is inadequate to apply the concept of synflorescences to the Bruniaceae. The most important arguments against it are (1) the resulting presence of renewal zones within one synflorescence and (2) the derivation of `proliferating synflorescences´ from originally monotelic synflorescences. As the studies of tree architecture have illustrated increasing sexuality expresses the gradual increase of a reproductive programme that first superposes the vegetative programme and finally may substitute it completely. Flowering woody shoot systems are thus characterized by two antagonistic developmental pathways, the vegetative which is characterized by the capacity of renewal and the reproductive which is characterized by the capacity of sexuality. Mainly they are clearly separated, but sometimes they interact or alternate pointing to a sectorially and/or rhythmically regulated meristematic activity of the apex concerned (Sell 1995).

4.3.3.1 Definition and delimitation. Taking the reproductive unit (RU) as the expression of the reproductive programme of the woody plant it is appropriate to define it as the largest repeated flowering unit of strictly caducous nature.

Reproductive units are parts of the RS and characterized by both their short life-time and the lack of any persistent shoot elements. They are delimited by persistent elements, the renewal zone (anthetic type; fig. 234: rz) and the parent stem continuing the shoot system above the RUs (ananthic type; fig. 234: is). In anthetic-sympodial shoot systems the RU corresponds to the terminal flower/inflorescence in the apical zone above the main renewal zone (fig. 236 az: black) and may be repeated on lateral shoots of any order of branches (`repeating shoots´). In ananthic-sympodial shoot systems the RU corresponds to each of the strictly caducous flowering lateral shoots in the branching zone (`inflorescence shoots´) below the main renewal zone (fig. 236 bz: black).

Outside the woody plants, RUs correspond to each of the overground flowering shoot systems in perennial herbs irrespective of being a synflorescence (fig. 208B_1) or a paraclade in the sense of Troll (B_2), and to the entire flowering plant in annual herbs (A). Considering the lacking branching zone in the herbal plants and the lacking renewal zone in the annual plants the latter can be interpreted as neotenic life forms (fig. 235). It is evident that the ontogenetic abbreviation of the plants´ architecture does not necessarily affect the structure of the next lower level of complexity, that is the RU.

The RU is largely identical with both synflorescences s.str. (see p. 251) and ephemeral `inflorescences´ sensu Van Steenis (1963) and Schröder (1987) (fig. 231:frame; fig. 213B). As they represent the largest repeated flowering unit of strictly caducous nature they may comprise one to several `florescences´ and `pseudoflorescences´ sensu Troll (1964b), `unités de floraison´ sensu Sell & Cremers (1994) and `uniflorescences´ and `conflorescences´ sensu Briggs & Johnson (1979) (fig. 231).

As regards the caducous nature of the RU the absolute life age is less important than the absolute lack of any elements renewing the vegetative shoot system. (1) Cauliflorous inflorescences e.g. producing flowers over several seasons before dying off would correspond to the definition while in case of *Anaxagorea dolichocarpa* (fig. 226D), where renewal shoots arise from the cauliflorous inflorescences, each of the single flowers would represent an individual RU. (2) The caducous nature of the RU must not be mixed up with a strictly reproductive nature. It merely points to the ephemeral character of all leaves and shoots which may appear within an individual RU (see definition of `vegetative´ by Schröder 1987, § 4.2.3.2).

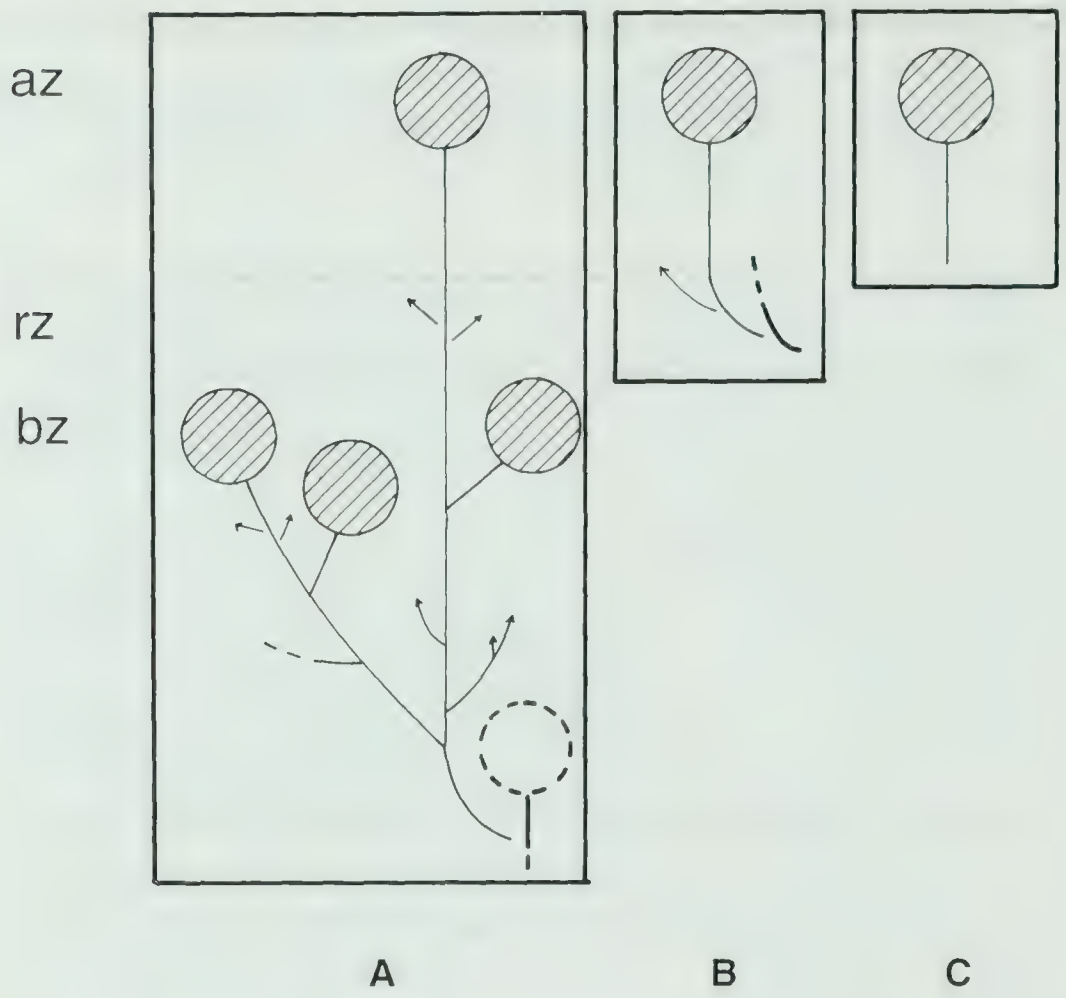


*Figure 235 - **The delimitation of reproductive units in plants of different life form**. The RU is defined as the largest repeated flowering unit of strictly caducous nature. In woody plants (A, e.g. anthetic type) several RUs may appear per RS. In perennial herbs (B) each of the overground flowering shoot systems terminates in an individual RU. In annual herbs (C) the entire flowering plant only produces one RU. The gradual lack of the branching (B) and renewal zone (C) in herbal plants may be interpreted as neoteny. It does not affect the structure of the RUs (hatched).*

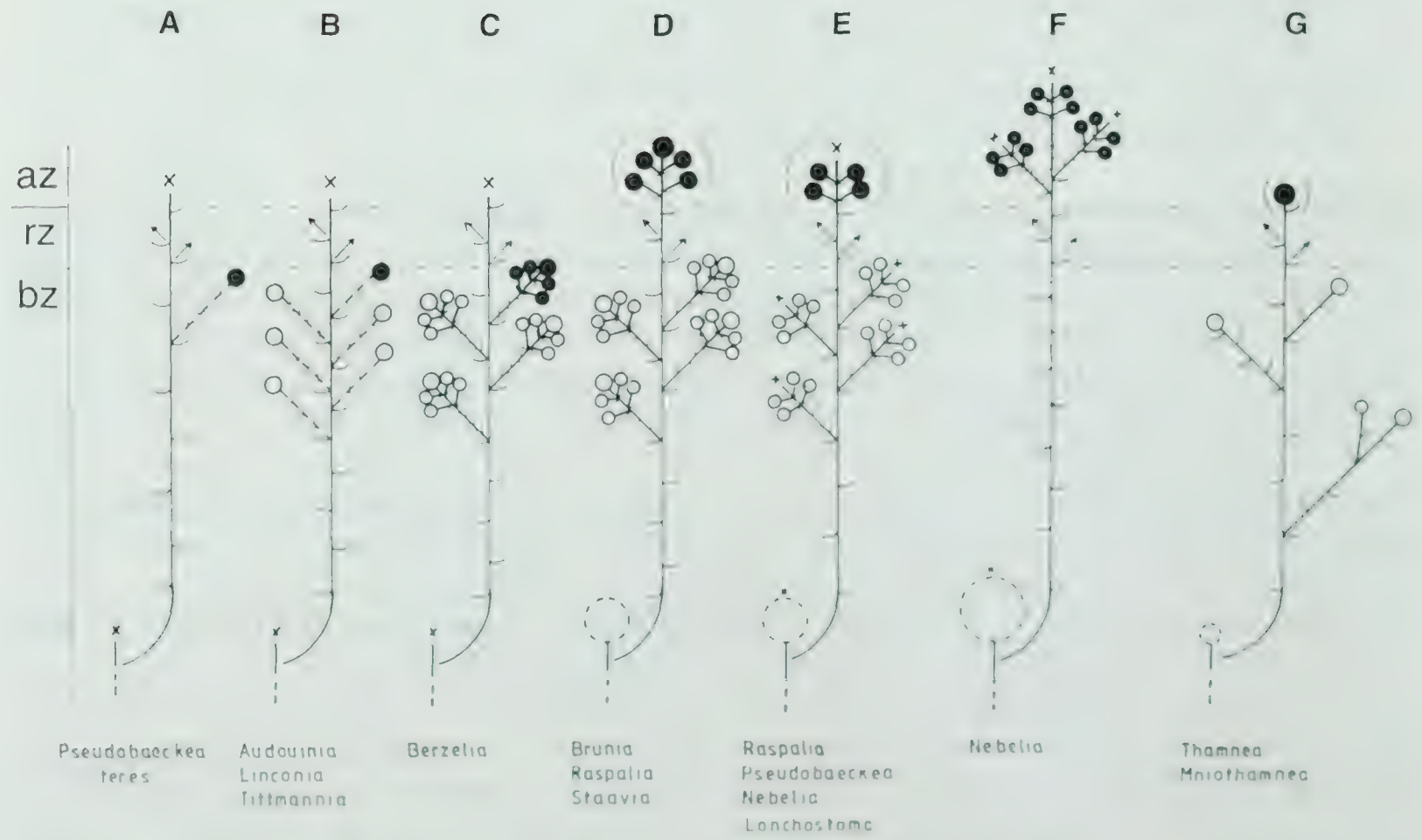


*Figure 236 - **Position and structure of the reproductive units in Bruniaceae**. The reproductive units (black) are delimited by persistent elements, the prospective woody parent stem in ananthic (A-C) and the renewal zone in anthetic sympodia (D-G). They correspond to (1) solitary flowers on bracteate short-shoots (A,B), (2) cephaloids (C,D), (3) truncate cephaloids ('heads') (E), (4) heterothetic double-'heads' (F) and (5) solitary flowers on leafy shoots (G) (see text)*

The characterization of the RU as the `largest repeated´ unit refers to the fact that inflorescences of different size may be delimited by persistent elements within one plant. The examples of *Berzelia albiflora* (fig. 66) and *Castanea sativa* (fig. 228) illustrate that not the absolute largest inflorescence delimited by a renewal zone corresponds to a RU, but the largest unit which in all cases is delimited by a renewal zone (D).

4.3.3.2 The reproductive units in Bruniaceae. Fig. 236 summarizes the reference systems and reproductive units (black) in Bruniaceae. Dependent on the position of the RUs ananthic-sympodial (A-C) and anthetic-sympodial genera appear within the family (D-G). Dependent on the structure of the individual RUs five groups are distinguishable.

(1) *Audouinia, Linconia, Tittmannia* (B) and *Pseudobaeckea teres* (A) always bear solitary flowers at the top of lateral bracteate short shoots.
(2) *Berzelia* (C), *Brunia, Staavia* and *Raspalia* p.p. (D) have determinate (`cephaloids´) and
(3) *Raspalia* p.p., *Pseudobaeckea, Nebelia, Lonchostoma* and *Nebelia* p.p. (E) indeterminate inflorescences (`truncate cephaloids´, `heads´).
(4) In *Nebelia fragarioides* and *N. stoekoei* (F) compound inflorescences appear which are composed of a terminal and numerous lateral `heads´ (heterothetic double-`heads´).
(5) *Thamnea* and *Mniothamnea* (G) again are characterized by solitary flowers which however terminate leafy shoots of different length.

Applying the definition of the RU to *Audouinia capitata* (fig. 204E) it becomes evident, that the spike-like inflorescence in fact corresponds to the dense aggregate of uniflorous short-shoots each representing the `largest repeated flowering unit of strictly caducous nature´ and thus an individual RU. The main arguments for the interpretation are (1) that the renewal of the shoot system usually arises from above the flowering zone and (2) that occasionally vegetative shoots appear among the flowering short-shoots (fig. 8A: svL). Besides, the divergent flowering sequence (fig. 6, 7B: arrows), the presence of numerous bracts below each flower, the occasional solitary position of a flowering short-shoot (fig. 8D) and the production of floral buds at its subterminal part (fig. 11B) support the interpretation that the `spike´ is not a single `proliferating´ inflorescence.

Reproductive units are thought to be comparable to each other (fig. 204E). Thus, each of the flowering short-shoots of *Audouinia capitata* is comparable to each of the lateral inflorescences of *Berzelia* and *Raspalia* and at the same time to each of the terminal inflorescences of *Raspalia* and *Lonchostoma*. The example illustrates that the position of the individual RU within the entire shoot system does not influence their morphological homology. Further examples demonstrating the only subordinate significance of the position of RUs are given by *Brunia albiflora* (fig. 66A-D) and *Nebelia paleacea* (fig. 115B:I,II), where the position of the RU is flexible in reference to the RS even within an individual plant. In this point the RS fundamentally differs from the RU where the position of the parts plays an essential role. The reason is that RUs - as flowers and fruits - are defined relative to their quality and not relative to their position. The only positional criterion that can be listed for both, RUs and flowers, is their strictly terminal position on caducous shoots or shoot tips. Nevertheless the individual RUs are identical structures and without doubt morphologically homologous to each other.

As the position of persistent elements plays a central role in delimiting the RU from the prospective woody part of the plant, changes of the branching pattern (monopodial/sympodial) and of the position of the renewal zone may directly influence the size of the RU (compare with fig. 216, 228).

- In *Nebelia fragarioides* and *N. stokoei* compound inflorescences (fig. 237A´,B´) appear above the renewal zone instead of simple ones (fig. 237A,B). They are `homotopous´ (same position) to the simple inflorescences in *N. sphaerocephala* and likewise represent the RU of the species concerned. But considering their formation in the course of evolution two different modes are possible (fig. 237). (A) Proceeding from an anthetic RS with sylleptic flowering lateral shoots (hatched) in the branching zone, the compound inflorescence could be the result of aggregation (*A*) causing an extreme internode inhibition (*I*in) in the distal part of the RS as well as the loss of the original renewal zone (*I*rz) and its functional substitution by lateral shoots from the branching zone (rz*). In

this case the zonation of the RS is changed and the terminal inflorescence enriched by flowering shoots from the branching zone. The new, superior RU* appears after the downwards displacement of the renewal zone and thus, in a strict sense, is not comparable to the simple RU. (B) On the other hand the compound inflorescence could also arise from a basipetalous enrichment (*In*) of the terminal inflorescence. In this case the structural change appears within the terminal inflorescence. It only concerns the caducous apical zone and thus would be comparable to the simple RU. It is thought that the latter way is realized in *Nebelia* because no transitional forms appear between simple and compound inflorescences. The example illustrates that the superposition of two developmental pathways, namely the plasticity of the RS (A) and of the RU (B), may result in analogous forms which, however, are homotopous and reflect the reproductive programme of the plant concerned. The consequent conclusion is that the RUs only reflect actual reproductive units but not necessarily homologous phylogenies.

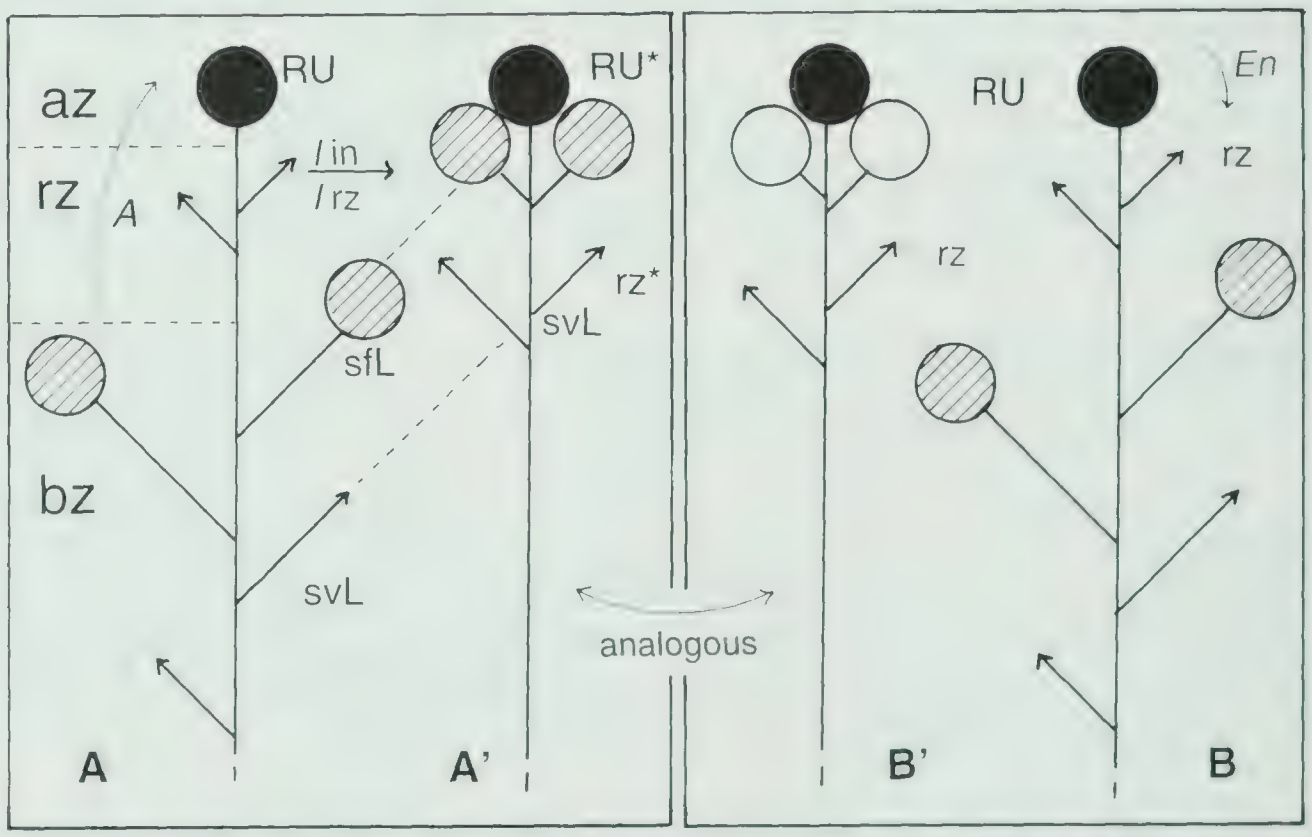


Figure 237 - ***Interaction between different levels of complexity illustrated in* Nebelia**. *Proceeding from an anthetic RS bearing flowering lateral shoots in the branching zone (A,B) terminal compound inflorescences may result by changes either concerning the RS-level (A': terminal aggregation of the flowering lateral shoots, loss of the renewal zone, functional substitution by vegetative shoots from the branching zone), or the RU-level (B': basipetalous enrichment of the terminal inflorescence). Note that in A' a superior RU (*) and a secondary rz (*) are formed both including lateral shoots from the branching zone.*

*A, aggregation, I*in, *inhibition of internodes, I*rz, *inhibition of renewal zone.*

- The genus *Lonchostoma* is characterized by terminal truncate RUs (fig. 238A',B') with the only exception of *L. esterhuyseniae*. This species occasionally shows 'proliferating synflorescences' caused by monopodial shoot connection (fig. 87). The question, whether *L. esterhuyseniae* represents a primitive or derived character state, can not be answered in a satisfactory manner (fig. 238). The presence of strictly terminal inflorescences in the remaining species of the genus, the occurrence of truncate inflorescences in *Raspalia* and the only rare appearance of 'proliferation' in *Lonchostoma esterhuyseniae* plead for the second case, namely to interpret the RU of *Lonchostoma* as a truncate inflorescence (B,B': *T*) which in *L. esterhuyseniae* occasionally shows proliferation in the sense of Troll. However, the presence of up to three prophylls in *L. myrtoides* and the general problem to accept 'proliferating synflorescences' sensu Troll in woody plants also allow a comparison with the 'false spikes' of *Audouinia capitata*. Then, the terminal inflorescence in *Lonchostoma* would in fact correspond to a cluster of lateral uniflorous short-shoots (A': RU*). As in *Castanea sativa* (fig. 228) the 'terminalization' would be caused by the inhibition of the apical part of the shoot system (*I*ap) and the displacement of the renewal zone (rz*). *L. esterhuyseniae*.

then, would be the only species that occasionally still demonstrates the original lateral position of the one-flowered short-shoots.

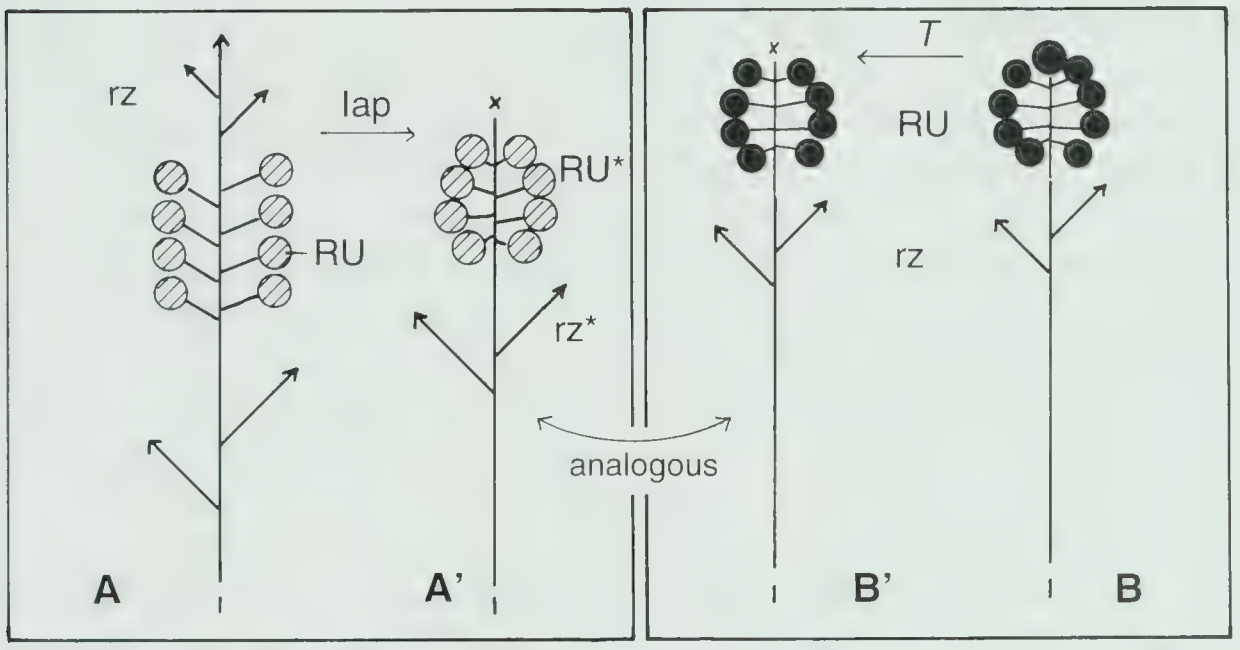


*Figure 238 - **Different interpretations of the terminal inflorescence in** **Lonchostoma**. Proceeding from a monopodial unit bearing lateral uniflorous short-shoots (A) a terminal inflorescence (A') appears after inhibition of the apical part of the shoot system and formation of a secondary renewal zone (rz*) from shoots of the branching zone. Proceeding from a terminal determinate inflorescence (B) the indeterminate form results from truncation (B': T). Note that in A the entire shoot system is involved in forming a superior RU (*) and a secondary rz (*), while in B the change only concerns the terminal RU. lap, inhibition of apex.*

4.3.3.3 Reproductive units in other plant groups. The delimitation of inflorescences in woody plants directly influences their homology. The inflorescence of e.g. *Sloanea monosperma* (Elaeocarpaceae) is taken as a polytelic synflorescence by Bayer (1994; fig. 217C), but following the present study it corresponds to an aggregate of uniflorous RUs each of which is monotelic in the terminology of Troll. The following list illustrates how the RU is applicable to selected examples of other plant groups.

- Referred to the concepts of Parkin (1914) and Pilger (1922) (§ 4.2.1) RUs would correspond to all inflorescences formed by the process of production (fig. 205: B-E; fig. 206: white) while those formed by segregation, in particular intercalary inflorescences, would correspond to a flowering shoot system bearing RUs (fig. 205: F-I; fig. 206: back). Bracteate indeterminate inflorescences might have evolved on both levels of complexity, production and segregation.
- Referred to the concept of Troll (e.g. 1964/69) (§ 4.2.2) RUs correspond to synflorescences s.str. which are defined as caducous inflorescences (fig. 208: A, B_1, C_{1-3}; fig. 213: A,B). A synflorescence s.l. would then correspond to a flowering shoot system bearing a series of synflorescences s.str.
- Referred to the studies of Sell & Cremers (1994) (§ 4.2.3.4), the RU may correspond to one UF or to more than one. The UF is a subunit of a caducous inflorescence and for that reason must not be mixed up with the subdivision of a flowering shoot system into individual RUs.
- Referred to the concept of Briggs & Johnson (1979) (§ 4.2.3.3; fig. 218) the RU corresponds to each of the Us in *Decaspermum paniculatum* (A), *Darwinia* spec. (D) and *Callistemon* spec. (E), to the entire determinate or truncate inflorescence of *Angophora* spec. (B,B'), to each of the Us and Cs respectively of *Eugenia* spec. (C), and to each of the Cs in *Darwinia* spec. (D') and *Melaleuca* spec. (F) In *Eugenia* and *Darwinia* it appears probable that the blastotelic-anauxotelic inflorescences have derived from auxotelic inflorescences Referred to the RU this would mean that e.g. the bell-shaped inflorescences of *Darwinia* spec. have developed from intercalary inflorescences and therefore correspond to a terminal aggregate of RUs each (compare with *Castanea sativa*, fig. 228; *Lonchostoma esterhuyseniae*, fig. A'). The same is true for *Eucalyptus* while *Eugenia* shows true

truncate inflorescences. Conflorescences sensu Briggs & Johnson (1979) thus might correspond to an individual RU or to an aggregate of individual RUs.

- In Scrophulariaceae, the shrubs of *Hebe diosmifolia* are characterized by lateral RUs which become terminal when the vegetative vigour fell short of a certain limit (fig. 214A-D). In contrast to them the herbs of *Veronica* are characterized by a terminal RU which may underlie truncation and proliferation (fig. 214E-H).
- In Hamamelidaceae, the RU corresponds to a simple raceme in *Parrotia* and to a single flower in *Distylium* (fig. 215: black).
- In Betulaceae, each of the male and female catkins represents an individual RU being densely aggregated in *Alnus glutinosa* and solitarily arranged in e.g. *Betula nana* (fig. 216A,D).
- In *Castanea sativa* (fig. 228) Gleißner (1998) found that the originally laterally arranged female inflorescences, each representing an individual RU, form a superior terminal inflorescence in adult plants. Terminalization here resulted from the gradual reduction from above and from the formation of a substitutive renewal zone from below.

Accepting the existence of different levels of complexity in woody plants the interpretation of inflorescence morphological data has to be reconsidered in each plant group; also in those where homologies appear to be clear. Because of the appearance of similar patterns on different levels of complexity, it is essential to analyse extended flowering shoot systems profoundly, to compare related species and to apply a largely unbiassed reference framework. Unexpected rearrangements should not be denied from the beginning but should stimulate discussion about the evolution of inflorescences.

4.3.4 The analogous nature of `proliferation´

The two different levels of complexity, the flowering shoot system and the inflorescence, both underly similar developmental processes (e.g. homogenization, Sell 1982). As a result very similar patterns might appear (Parkin 1914, fig. 205; Hamann 1958/60, fig. 214; Briggs & Johnson 1979; Sell 1982, fig. 220):

The examples of *Audouinia* and *Lonchostoma* in particular point to the analogous formation of `proliferating inflorescences´, which appears to be possible on both the RS- (A) and the RU-level (B).

- Proceeding from the level of flowering shoot systems (fig. 239A) `intercalary´ inflorescences sensu Parkin (1914) may result. An indeterminate shoot system (A) bearing determinate sylleptic flowering lateral shoots (sfL) merges into a `spike´ (A´) by reduction, homogenization and aggregation. The main shoot always remains unchanged and continues to grow on in a monopodial manner.
- Proceeding in contrast from the level of the reproductive unit (fig. 239B) `proliferating synflorescences´ sensu Troll (1964) may result. A terminal determinate inflorescence (B) also merges into a `spike´ (B´) by truncation and homogenization. In doing so the apex of the main shoot is changed. It may reactivate the capacity to grow on and then `proliferates´.

Both forms are realized in nature. While intercalary inflorescences only appear in woody plants being composed of lateral shoots of the branching zone, proliferating synflorescences (also or only?) appear in perennial and annual herbs always involving terminal units. To distinguish both forms in woody plants the relative position of the renewal zone and inflorescence has to be studied showing whether the branching zone below the renewal zone is involved in the inflorescence (A´´) or only the apical zone above it (B´´).

Troll interpreted all proliferating inflorescences in the second sense (B) irrespective of the life form of the plant and the level of complexity. An important argument was the repeated existence of transitional forms between terminal and proliferating synflorescences (e.g. Weberling & Troll 1998: 50). However, these forms only illustrate the existence of a morphological series but do not determine the direction of evolutionary pathways. `Proliferating synflorescences´ in woody plants can also be interpreted as `intercalary inflorescences´. However, in doing so the morphological results and systematic conclusions will change.

Troll explained his view by numerous examples both from annual and woody plants. Concerning the latter the pineapple is a well known example. However, looking at a longitudinal section it is clear that the apical leafy tuft is not part of the inflorescence, but an individual new rosette which, besides, is able to regenerate the plant for which reason it is also used for propagation. The Myrtaceae *Callistemon* and

Melaleuca, further well known examples, were already cited by Van Steenis (1963) as twigs `covered with laterally arranged uniflorous inflorescences´. Sell (1982) and Briggs & Johnson (1987) confirmed this view. Both were influenced by Troll´s concept and did not completely refuse the appearance of proliferating synflorescences, but discussed the analogous nature of proliferation (fig. 276).

As a preliminary conclusion, proliferation in woody plants might be largely reduced to monopodially connected shoot chains with laterally arranged flowers/inflorescences (fig. 239A). The so-called `primitive´ angiosperms and many other woody plant families would then have relatively primitive instead of highly derived inflorescences. On the other hand the examples of proliferating synflorescences in herbal plants appear to confirm Troll´s view. It is therefore imaginable that the two forms of `proliferation´ would represent two different levels of evolution (see fig. 214, 240). Proceeding from originally `proliferating´ woody shoot systems, namely monopodial units, a terminalization might have taken place by neoteny resulting in a terminal determinate inflorescence. Further neotenous reductions result in herbal life forms which might originally have been characterized by terminal inflorescences. `Proliferation´ in the sense of Troll then had occurred in a few plant groups for biological reasons which still have to be studied in the future.

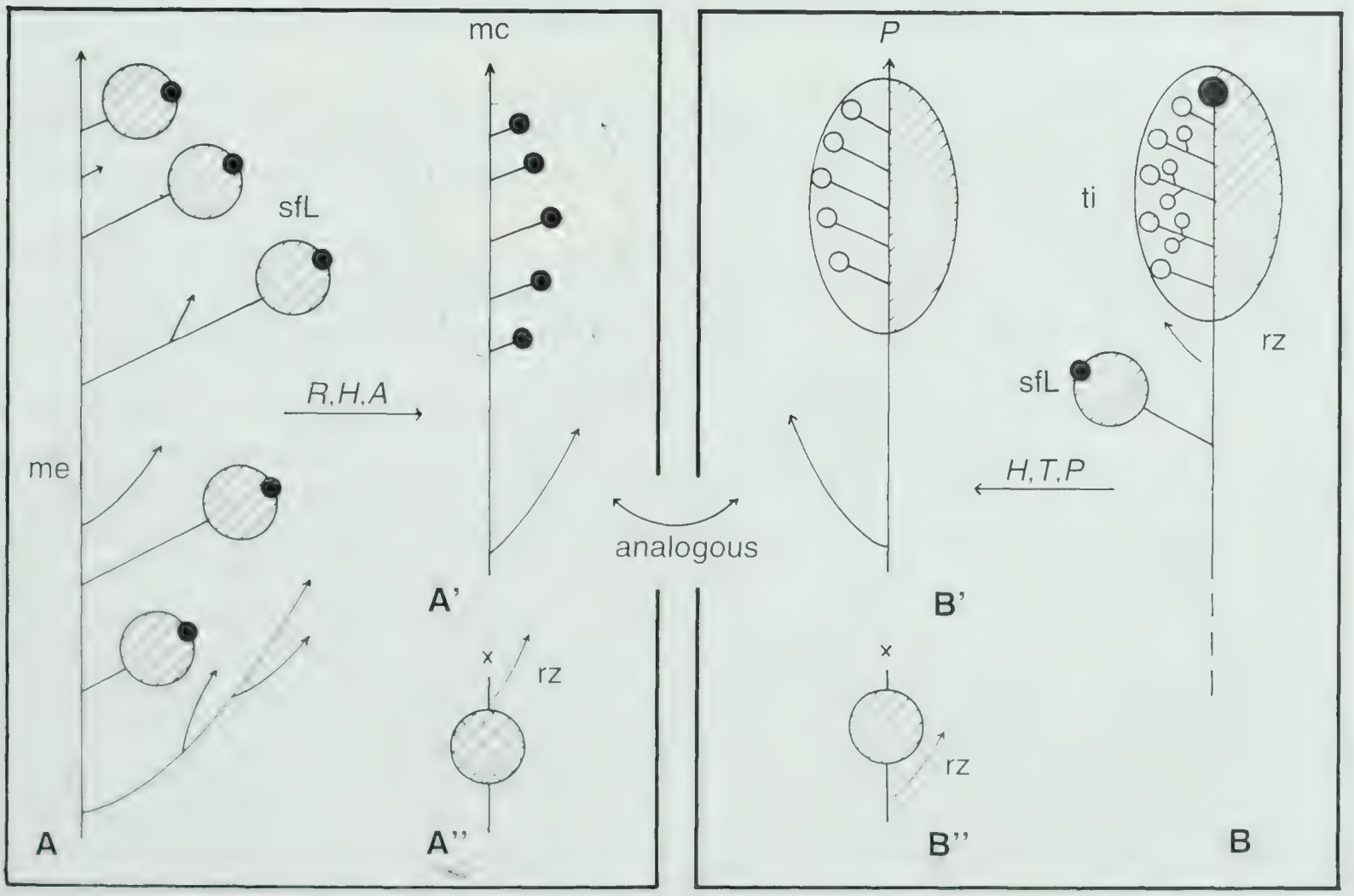


Figure 239 - `Proliferating inflorescences´ on different levels of complexity in woody plants. A, A´: proceeding from an indeterminate shoot system bearing determinate sylleptic flowering lateral shoots a `spike´ results by reduction, homogenization and aggregation; the main shoot remains unchanged and continues to grow on. B, B´: proceeding from a terminal determinate inflorescence a `spike´ also results by truncation and homogenization; the secundarily open apex of the main shoot may return to vegetative growth and proliferate. A´´, B´´: the relative position of the renewal zone above (A´´) or below (B´´) the inflorescence may indicate whether the `spike´ is comparable to an aggregate of uniflorous lateral short-shoots (A, A´) or to a terminal truncate inflorescence (B, B´). *A, aggregation, P, proliferation, R, reduction.*

4.3.5 A short comment on the evolution of inflorescences

The `brunioid´ RS does not include any phylogenetic information. However, it might be interesting in the present context to reconsider the evolution of inflorescences in woody plants.

Until now, the origin of inflorescences is an open question (Parkin 1914, Zimmermann 1965, Stebbins 1973, Takhtajan 1973, 1991, Weberling 1983a). However, with the exception of only a few authors (e.g. Pilger 1922, Briggs & Johnson 1979) who proceeded from a flexible, not strictly determinated apex, there is a broad agreement that the terminal flower represents the primitive stage. Weberling´s exclamation "*We need primitive inflorescences, urgently*" (1988b: 688) raises the question of how to define primitive characters in inflorescences. Since fossil evidence and molecular studies are largely lacking arguments should predominantly come from primitive angiosperms and growth form morphology.

Recent morphological and molecular studies challenge the classical view that the early angiosperms were large and woody plants (Kubitzky et al. 1993, Crane et al. 1995, Judd et al. 1999). Instead it is suggested that they might have been short-lived semi-herbs. The basal habit, however, is equivocal; magnoliids and `paleoherbs´ in particular emphasize the great diversity of life forms among the primitive groups. For this reason it is tenable to assume that also the position of the inflorescences was flexible in the basal groups. It is furthermore speculated that the early angiosperms very rapidly radiated into trees, lianas and herbs each being characterized by individual branching patterns.

Referring to the concept of neoteny, which is widely accepted to be fundamental, woody plants show a less derived life form than herbs. Likewise monopodial branching patterns and indeterminate apices appear to represent more primitive stages than sympodial branching patterns and apices merging into a terminal flower/inflorescence.

If this is accepted the ontogenetic stages explained in fig. 233 could be taken as phylogenetic recapitulations. The most primitive flowering stage of a woody plant could then be compared with the `pubescent´ stage (C) of the generalized life cycle of the Bruniaceae, while the adult stages (D-E´) all result from different degrees of ontogenetic abbreviations.

However, the phylogenetic reconstruction by means of ontogenetic stages is not undisputed. It includes many sources of error as simple structures may represent both a primitive and an advanced, secondarily reduced stage. Holländer & Jäger (1994) pointed to the importance of heterobathmy to explain supposed derived characters in primitive plants and vice versa. Jäger (1980) also thought that the change from zoogamy to secondary anemogamy in trees may influence the activity of the apices resulting in monopodial shoot connections. Both might be true of individual taxa but considering the monopodial shoot connection to be primitive heterobathmy has not to be used in such a large amount.

A second reason to refuse the given reconstruction may be the argument that shoot systems with long-shoot short-shoot dimorphism are derived because of their high degree of division of labour. However, the question arises whether the division of labour is a newly evolved capacity or whether it reflects a primitive stage. Referred to the generalized life cycle of the Bruniaceae (fig. 233) anthetic and ananthic shoot systems have to be distinguished.

- In ananthic plants division of labour always and necessarily arises when the plant becomes sexualized because only specialized `inflorescence shoots´ are able to flower. This is an immanent feature of ananthic sympodia and has scarcely to do with selection towards a higher grade of division of labour.
- In anthetic shoot systems the division of labour usually appears as a typical accompaniment of ontogenetic younger stages while it gets lost in adult plants. It is possible to interpret this situation by the early (premature?) impulse of sexuality. Flowers are already produced at a time when the vegetative body of the plant still has to be extended. For that reason the most vigorous shoots including the main axis remain vegetative while weaker shoots already start to flower. As soon as the sexual impulse also covers the dominant shoot the division of labour gets largely lost.

In both types the shoot dimorphism proves to be primitive. It is preserved in ananthic plants for immanent reasons, while it might be given up in the adult phase of anthetic plants. Because of its multifunctionality it might have been intensified in the course of evolution appearing derived at the present time.

However, adult plants occasionally show another form of division of labour which might be taken as being derived. As fig. 233E,E´ shows, strictly reproductive and strictly vegetative SGUs may appear in adult plants representing a division of labour on the superior level of a several seasons old shoot system. The primary division of labour caused by long-shoot short-shoot dimorphism within an individual SGU is paralleled by a derived division of labour caused by a SGU dimorphism.

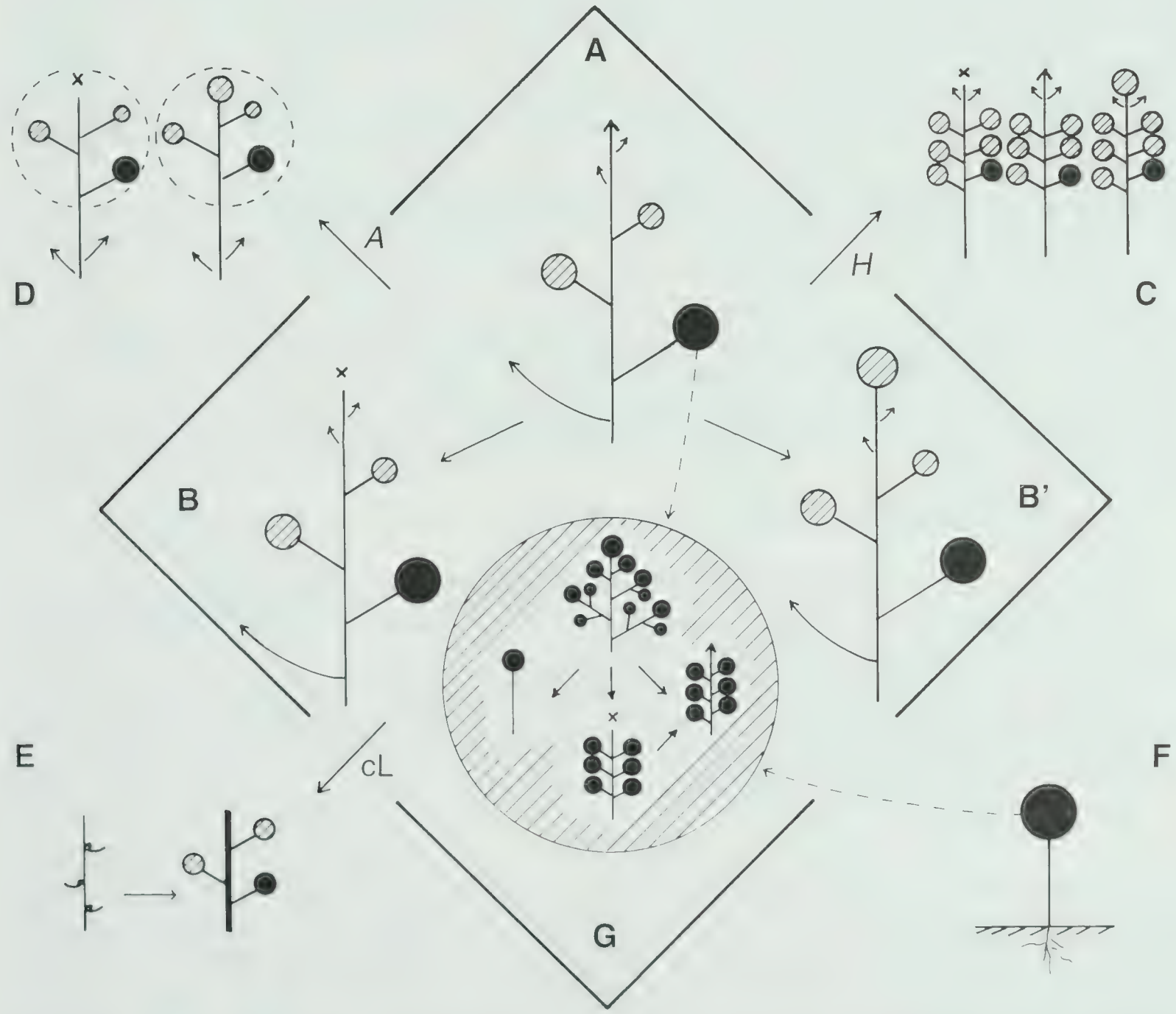


*Figure 240 - **Preliminary model concerning the evolution of inflorescences**. Proceeding from a sylleptically branched woody shoot system growing on monopodially (A) sexualization always starts on weak lateral shoots. The lateral position of all individual RUs is preserved in ananthic-sympodial shoot systems (B), while in anthetic sympodia (B´) a terminal RU results from the transfer of the sexual impulse to the apex of the dominant shoot (`terminalization´). The shoot system underlies similar developmental processes as individual RUs, e.g. homogenization (C) and aggregation (D), both being able to form superior flowering patterns which may mask the size of the individual RUs. Woody plants of temperate climates show cataleptic instead of sylleptic branching (E). In herbal plants the branching and renewal zones are lacking (F). For that reason the entire plant only bears a single terminal RU. The individual RUs of both woody and herbal plants pass similar evlutionary lines proceeding from a determinate inflorescence to indeterminate types of different polytelic degrees (G; see fig. 212). Note that proliferating shoot systems are thought to be primitive in woody and derived in herbal plants, while the terminal position of RUs appears to be derived in woody and original in herbal plants.*
A, aggregation, cL, cataleptic lateral shoot.

Irrespective of the life form of the plants, reproductive units in woody and herbal plants underlie the same developmental pathways (fig. 240F). They are always arranged terminally relative to the main axis of the RU and develop basipetally dependent on the degree of the sexual impulse. For that reason they originally bear a terminal flower. In the course of evolution manifold RUs have evolved differing in the number and position of flowers. Compound inflorescences may result from rich-flowered systems being subdivided by the elementary processes of razemization and homogenization or from simple inflorescences being enriched by further inflorescences (see fig. 212). The arrangement of the subunits within an individual RU shows similar patterns as the arrangement of RUs within a woody shoot system because identical positional programmes control both the RS and the RU.

Figure 240 summarizes the short speculative comments on the evolution of inflorescences. It is evident that the different evolutionary level of the inflorescences in woody (A-E) and herbal plants (F-G) has to be considered.

In woody plants the flowering impulse appears to start at lateral branches (A). The main axis grows on for several seasons (monopodial mode) or becomes regularly substituted by lateral renewal shoots (B; sympodial mode). In anthetic-sympodial shoot systems terminalization of the flowering impulse caused by neoteny results in a terminal inflorescence (B´). Adult plants of both types, ananthic and anthetic, may show a superior division of labour caused by SGU dimorphism. Flowering shoot systems bearing RUs (A-E) underlie the same developmental processes as individual RUs (F-G). Homogenization (C: *H*) for example may produce patterns similar to those of inflorescences (G) and aggregation (*A*) may result in false terminal units being composed of several instead of one RU (D). As a general cocnlusion

- indeterminate flowering shoot systems are thought to be primitive in woody plants (A,B) and derived in herbs (G),
- terminal inflorescences appear to be derived in woody plants (B´) but original in herbs (G),
- `proliferating inflorescences´ may correspond to flowering monopodia (A,C) or to RUs whose apical meristem has secondarily become reactive (G) and
- flowering shoot systems being subdivided in several flowering entities may correspond to woody shoot systems bearing several RUs (A-B´) or to an individual caducous RU bearing partial inflorescences (G).

5

Systematic conclusions from inflorescence morphology

Tab. 2 summarizes the main characters of the flowering reference systems of each of the 63 species examined. In detail (I) the organization of the individual RU and (II) the grade of aggregation between individual RUs are listed as well as (III) the orders of branches of the RU-bearing shoots, (IV) the position of the individual RUs referred to the SGU, (V) the peculiarities of leaf metamorphosis, (VI) the features of the bracts, (VII) the organization of the sylleptic flowering lateral shoots of the 1st order of branches bearing more than one RU, (VIII) the presence of sylleptic flowering and (IX) sylleptic vegetative lateral shoots in the branching zone of the RS, (X) the developmental behaviour of the renewal shoots in time referred to the parent axis, (XI) the mode of SGU-connection and (XII) the type of the RS.

5.1 Position and organization of the individual RUs in Bruniaceae

Relative to inflorescence morphology the most important characters are the organization and position of the individual RUs (tab. 2: I, IV, XII).

5.1.1 Position of the RU

According to the position of the RU three groups are distinguished (tab. 3)

- strictly ananthic (I/1)
- flexible (I/2)
- strictly anthetic including monopodial units (I/ 3a) or showing a strictly sympodial branching pattern (I/ 3b).

The position of the RUs is not uniformous within the individual genera (fig. 243). This might point to repeated changes either from flexible to both ananthic and anthetic sympodia or from ananthic via flexible to anthetic sympodia.

Briggs & Johnson (1979) hold the opinion that the flexible condition of the terminal meristem of an individual SGU would reflect the most primitive stage in the evolution of flowering woody plants, while both the strictly blastotelic and anthotelic conditions would reflect specialization (§ 4.2.3.3). Following them *Brunia* and *Nebelia* (tab. 3: I/2, fig. 243: dotted frame) would include the most primitive forms relative to the organization of the shoot system. The remaining genera would be more advanced either showing both kinds of specialization (e.g. *Thamnea, Raspalia*) or exclusively ananthic (e.g. *Berzelia, Audouinia*) or anthetic sympodia (e.g. *Staavia*).

However, in Bruniaceae an alternative interpretation is likewise reasonable. Proceeding from an ancestor bearing RUs exclusively at leafy lateral shoots, evolution could have progressed either towards specialization or towards terminalization of the flowering impulse based on neoteny. The first would have resulted in ananthic sympodia bearing heteromorphic lateral shoots, namely leafy vegetative shoots and bracteose inflorescence shoots (e.g. *Berzelia, Audouinia*), the second in anthetic sympodia bearing homomorphic lateral shoots repeating the flowering parent shoot (e.g. *Thamnea, Raspalia*). The flexible condition would then represent the transitional stage between the original indeterminate and advanced determinate condition and not a primitive stage.

*Table 2 – **Characters of the reference systems in Bruniaceae** [1])*

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Audouinia												
A. capitata	1	4	2	1	2	2	1	1	1	2	1-2	1
Berzelia												
B. abrotanoides	2	2-3	1	1	2	2	2	1	1	2	1 ?	1
B. arachnoidea	2	3	2	1	2	2	1	1	1-2	2	1	1
B. burchellii	2	2-3	2	1	2	2	1	1	1	1	1	1
B. commutata	2	2-3	1	1	2	2	1	1	2	1	2	1
B. ecklonii	2*	2	2	1	2	3	2	1	1	2	2	1
B. galpinii	2*	2	2	1	2	2	2	1	2-3	2	2 ?	1
B. incurva	2	3	2	1	2	2	1	1	3	1	1	1
B. intermedia	2*	2	2	1	2	2	1	1	2	2	2	1
B. lanuginosa	2*	2-3	1	1	2	2	1	1	1	2	1	1
B. rubra	2*	3	3	1	2	2	-	1	1	2	2	1
B. spec.	2*	2-3	2	1	2	2	1	1	1	1-2	1 ?	1
Brunia												
B. albiflora	2	3	5	2	2	3	1-2	1	1	3	1	2
B. alopecuroides	2	3	2	1	2	2	1	1	1	2	1	1
B. laevis	2*	2	2	1	1	3	2	1	1	2	2 ?	1
B. macrocephala	2*	1-2	6	3-4	1	3	3	2	1-2	2	3	2
B. neglecta	2*	2	4	2	1	3	2	1	1	2	2 ?	2
B. nodiflora	2	2	4	2	1	3	2	1	1-2	3	1	2
B. stokoei	2	3	2	1	2	3	1	1	2-3	2	1	1
Linconia												
L. alopecuroides	1	4	2	1	2	1	1	1	2-3	1	1 ?	1
L. cuspidata	1	4	2	1	2	1	1	1	3 ?	1	1	1
Lonchostoma												
L. esterhuyseniae[a]	3+	-	7	4	2	1	-	3	3	1-4	2	2
L. esterhuyseniae[b]	1	4	3	1	2	2	-	3	3	1-4	2	1
L. monogynum	3	2	6	3	2	1	-	2	3	1-4	3	2
L. myrtoides	3	-	7	4	2	1	-	3	3	1-4	3	2
L. pentandrum	3	-	7	4	2	1	-	3	3	1-4	3	2
L. purpureum	3	-	7	4	2	1	-	3	3	1-4	3	2
Mniothamnea												
M. bullata	5	1-2	4	2	1	1-2	2	1	1	2	2	2
M. callunoides	5	2-3	1 ?	1?	1	1-2	2	1	1	2 ?	2?	2 ?
Nebelia												
N. fragarioides	4	2	6	3-4	1	3	-	2-3	1-3	1-2	3	2
N. laevis	3	2-3	5	2	1	3-4	3	1	2-3	1-2	2	2
N. paleacea	3	2-3	4	2	1	4	2	1	2-3	1-2	2	2
N. sphaerocephala	3	2	6	3	1	2-3	-	1	1	2	3	2
N. stokoei	4	2	5	3	1	3	3	1	1	2	3	2
Pseudobaeckea												
P. africana	3	3	5	3	2	2	3	1-3	3	2	3	2
P. cordata	3	2-3	4	3	1-2	1-2	3-2	1	2-3	1	2-3	2
P. teres	1	-	1 ?	1	2	2	-	1	1	1-2	1	1

Table 2 (cont.)

Raspalia												
R. angulata	2*	2	5 ?	2 ?	1	1	2	1	2	2 ?	2	2 ?
R. globosa	2	2	6	3	1	1	-	1	3	1	3	2
R. microphylla	2	2	5	2	1	1	2	1	2	2	1	1 ?
R. phylicoides	2*	2	6	2	1	1	-	1	2	1-2	2	2
R. sacculata	3	2	5	3	1	1	3	1	3	1	3	2
R. schlechteri	2*	2	1	1 ?	1	1	2	1	3	2	1 ?	1 ?
R. staavioides	3*	2	6	3	1	2	-	1	3	1	3	2
R. stokoei	3	1-2	6	3-4	1	1-2	-	2-3	3	1	3	2
R. trigyna	2	2	5 ?	2 ?	1	1	3	1	3 ?	2	1-3	2 ?
R. variabilis	2*	2	5	2	1	1	3	1	2-3	2	2	2
R. villosa	3	2	5	3	1	1-2	3	1	3	1	3	2
R. virgata	3	2	6	3	1	1-2	-	1	3	1	3	2
Staavia												
S. capitella	2	2	6	3-4	1	3	-	2	3	1	3	2
S. dodii	2	2	6	3-4	1	4	-	2	3	2-4	3	2
S. dregeana	2	2	6	4	1	3	-	1-2	3	1,4	3	2
S. glutinosa	2	2	5	3-4	1	4	3	1-2	3	1	3	2
S. radiata	2	2	6	3-4	1	3-4	-	2	3	2	3	2
S. verticillata	2	1	6	2-3	1	3	-	1	2-3	1-2	2	2
S. zeyheri	2	4	5	3	2	3	3	1	3	1	3	2
Thamnea												
T. diosmoides	5	2	5	3	1	3	3	2-3	1-2	1	2	2
T. gracilis	5	1	5 ?	2 ?	1	2-3	-	1	2	2 ?	3 ?	2 ?
T. hirtella	5	1	6 ?	2 ?	1	3	-	1-2	2	2	1 ?	2 ?
T. massoniana	5	2	5	3	1	3	3	1-3	1-3	1	3	2
T. thesioides	5	1	2	1	1	2	2	1	2	2 ?	1?	1 ?
Tittmannia												
T. esterhuyseniae	1	4	2	1	2	2-3	1	1	3	3	1	1
T. laevis	1	2,4	2 ?	1	2	2	1	1	1-2	2	2 ?	1
T. laxa	1	2,4	2 ?	1	2	2	1	1	1-2	2?	2	1

[1] *explanations:*

***I**, organization of the individual RU: **1**, solitary flowers at the top of bracteate short-shoots, **2**, cephaloids (*presumed), **3**, truncate cephaloids (*presumed; + occasionally `proliferating´), **4**, compound inflorescences composed of truncate cephaloids, **5**, solitary flowers at the top of leafy shoots. **II**, grade of aggregation between individual RUs: **1**, not aggregated, **2**, loosely aggregated, **3**, aggregated, **4**, densly aggregated pretending a superior unit. **III**, orders of branches of the RU-bearing shoots: **1**, 3rd to 1st, **2**, 2nd and 1st, **3**, 1st only, **4**, 3rd to 0, **5**, 2nd to 0, **6**, 1st to 0, **7**, 0 only. **IV**, position of the individual RUs referred to the SGU: **1**, lateral only, **2**, lateral and facultatively terminal, **3**, lateral and obligately terminal, **4**, terminal only. **V**, leaf metamorphosis: **1**, continuously, **2**, abruptly. **VI**, bracts: **1**, leafy, **2**, bracteose, **3**, involucral, **4**, petaloid. **VII**, organization of the sylleptic flowering lateral shoots of the 1st order of branches bearing more than one RU: **1**, always indeterminate, **2**, indeterminate and determinate, **3**, always determinate. **VIII**, presence of sylleptic flowering lateral shoots in the branching zone of the RS: **1**, always present, **2**, rare, **3**, lacking. **IX**, presence of sylleptic vegetative lateral shoots in the branching zone of the RS: **1**, always present, **2**, rare, **3**, lacking. **X**, developmental behaviour of the renewal shoots in time referred to the parent axis: **1**, cataleptic, **2**, sylleptic vegetative, **3**, sylleptic forming floral buds, **4**, sylleptic flowering. **XI**, mode of SGU-connection: **1**, repeatedly monopodial, **2**, monopodial and sympodial, **3**, strictly sympodial. **XII**, type of the reference system: **1**, ananthic-sympodial, **2**, anthetic-sympodial*

Lonchostoma [a/b]: different interpretations possible (see text).

*Table 3 – **Organisation and position of the reproductive units in Bruniaceae** [1]).*

	I / 1	I / 2	I / 3	
II / 1	**Audounina** A. capitata **Linconia** (2 spec.) **Pseudobaeckea** P. teres **Tittmannia** (3 spec.)			
II / 3	**Mniothamnea** M. callunoides **Thamnea** T. thesioides		M. bullata T. gracilis T. hirtella T. diosmoides	T. [illegible]
II / 2	**Berzelia** (11 spec.) **Brunia** B. alopecuroides B. stokoei B. laevis **Raspalia** R. microphylla R. schlechteri R. trigyna	B. albiflora B. neglecta B. nodiflora	R. angulata R. phylicoides R. variabilis **Staavia** S. verticillata	B. [illegible] R. [illegible] S. [illegible]
II / 3		**Nebelia** N. laevis N. paleacea	**Pseudobaeckea** P. cordata	N. [illegible] P. [illegible] **Raspalia** (3 spec.) **Lonchostoma** L. [illegible] L. [illegible] L. [illegible] L. [illegible] L. [illegible]
II / 4				**Nebelia** N. [illegible] N. [illegible]

[1]) *explanations:*

***I**, position of the individual RUs referred to the RS: **1**, exclusively lateral (ananthic sympodia), **2**, lateral and facultatively terminal (flexible condition), **3**, always terminal (anthetic sympodia); grey: strictly sympodial, white: monopodial units inserted (in the latter case individual SGUs are indeterminate; this case must not be mixed with the true flexible condition in I/2).*

***II**, organization of the individual RUs: **1**, solitary flowers at the top of bracteose short-shoots, **2**, cephaloids, **3**, truncate cephaloids, **4**, inflorescences composed of a terminal and several lateral truncate cephaloids, **5**, solitary flowers at the top of leafy shoots.* *?: different interpretations possible (see text).*

5.1.2 Organization of the RU

According to the organization of the RU four groups were distinguished (tab. 3)

- `*Audouinia*-group´ (II/1)
- `cephaloid-group´ (II/2)
- `truncate cephaloid-group´ (II/3,4)
- *Mniothamnea* and *Thamnea*. (II/5

With only few exceptions, all species of an individual genus show the same inflorescence structure.

Raspalia is the only genus that bears both determinate and indeterminate inflorescences (fig. 241 D, E) and thus represents an example of the often found transition from monotelic to polytelic inflorescences by truncation (*T*). It is generally accepted that truncate forms derived from determinate inflorescences. For that reason *Raspalia* p.p., *Nebelia, Pseudobaeckea* and *Lonchostoma* (except *L. esterhuyseniae*?) (fig. 241E,F) are thought to show more advanced inflorescences than *Berzelia, Brunia, Staavia* and *Raspalia* p.p. (A,D).

The compound RUs in *Nebelia fragarioides* and *N. stokoei* (fig. 241F) are taken to represent a more advanced stage than the simple RUs of the remaining *Nebelia* species (§ 4.3.3.2, fig. 237).

As regards the genus *Lonchostoma* the situation is not clear. *Lonchostoma esterhuyseniae* (*G*) resembles *Audouinia* in occasionally showing `proliferating inflorescences´. However, in contrast to *Audouinia*, renewal shoots always arise from below the inflorescence even if vegetative meristems are present above the flowers. As already discussed in fig. 238, the terminal truncate inflorescence, representing the RU of the genus, could have evolved from a terminal cephaloid or from an aggregate of several individual uniflorous RUs. Thus, *Lonchostoma esterhuyseniae* could be either the most advanced or the most primitive species of the genus. In the first case *Lonchostoma* could be derived from *Raspalia* or *Pseudobaeckea* supposing that the terminal inflorescence would represent a single terminal truncate RU (fig. 241G: right). In the second case *Lonchostoma* could be derived from the `*Audouinia*-group´ supposing that the terminal inflorescence in fact would have evolved from an aggregate of lateral RUs (G: left). The latter could be supported by the fact that the inflorescence axis does not break off after fruit fall but persists for several seasons (fig. 83B, 85A), perhaps demonstrating its phylogenetic origin from the persistent woody shoot system. If this is true the same interpretation has to be applied to the RUs of *Pseudobaeckea cordata* and *P. africana* whose inflorescences also show persistent axes (fig. 122, 124, 127A). Though *L. esterhuyseniae* shares the superior ovary and the pseudosympetaloid corolla of the remaining *Lonchostoma* species, it has to be proved whether it is in fact correctly placed in the genus. Besides the rare `proliferation´ it markedly differs from the remaining species relative to pollen morphological data. Furthermore, the species is known from only a single locality in the Riviersonderend mountains (Strid 1968, Scott 1989) more than 100 miles southeast of the localities of the remaining species in the Clanwilliam/Ceres area.

The morphological interpretation of the uniflorous RUs is likewise not clear. The flowering short-shoots of *Audouinia, Linconia, Pseudobaeckea teres* and *Tittmannia* (fig. 241B) are similar to *Berzelia* (A) whose cephaloids also terminate bracteose lateral shoots. They could have emerged from a common ancestor (?) or from each other by enrichment (En) or vice versa by numerical reduction (R). The interpretation of the uniflorous RUs in *Thamnea* and *Mniothamnea* (C) is even more difficult. As the shoot systems do not show any specialization the appearance of solitary flowers at the top of leafy shoots could represent a very primitive stage. On the other hand, the minute flowers particularly in *Mniothamnea* could also point to inbreeding and secondary reduction of an originally more extended RU.

The morphological discussion leaves many questions open (fig. 241). In particular it is not clear which kind of inflorescence would characterize the basal flowering conditions in the family. On the supposition that truncation (*T*) and terminalization (*Te*) represent advanced stages, only the *Audouinia*- (B), *Thamnea*- (C) and *Berzelia*-group (A) come into question. Among them *Berzelia* appears to have a central position, but *Audouinia capitata* is thought to have the most primitive characters in the family. The considerable differences between the three presumedly basal groups could also point to a common ancestor which could have been characterized by an indeterminate shoot system bearing determinate few-flowered inflorescences at leafy lateral shoots.

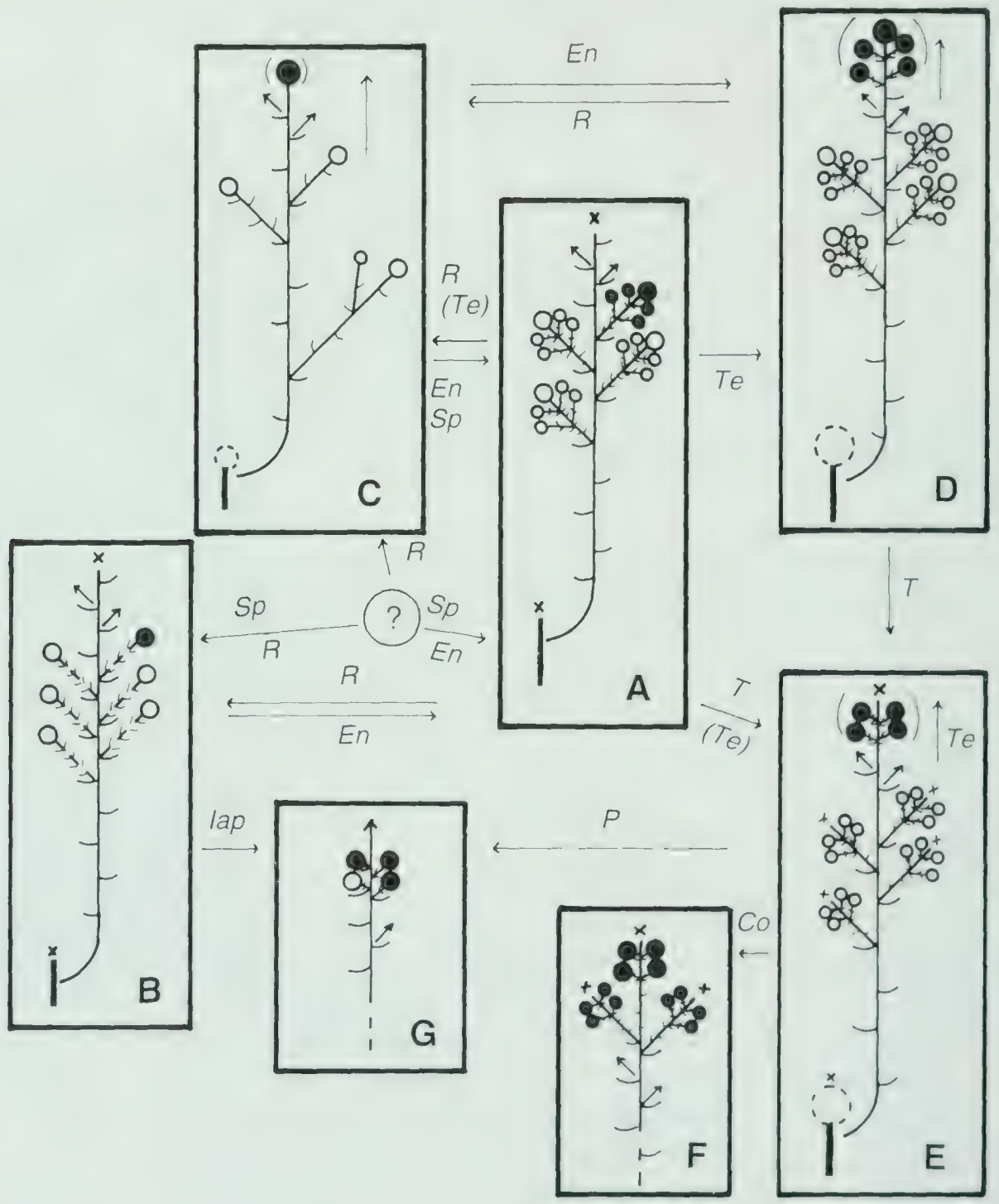


Figure 241 - ***Position and organization of the RUs in Bruniaceae***. *A*, Berzelia, *B*, Audouinia, Tittmannia, Pseudobaeckea teres, Linconia, *C*, Thamnea, Mniothamnea, *D*, Brunia, Staavia, Raspalia *p.p.*, *E*, Raspalia *p.p.*, Nebelia *p.p.*, Pseudobaeckea *(except* P. teres*)*, Lonchostoma *(except* L. esterhuyseniae*)*, *F*, Nebelia fragarioides, N. stokoei, *G*, Lonchostoma esterhuyseniae.
Compare with text.

Co, increasing complexity of the RU, Iap, inhibition of apical part, P, proliferation, R, reduction, Sp, specialization, Te, terminalization,black: RU (note that the right and left side in G show different RUs dependent on the different evolutionary ways in discussion).

5.2 The intergeneric relationships of the Bruniaceae

Table 3 illustrates that in Bruniaceae two independent morphological characters are correlated with each other and with the branching behaviour of the shoot system.

- Ananthic-sympodial shoot systems (I/1; dark grey) exclusively bear uniflorous RUs (II/5,1) or cephaloids (II/2). They never show a regular sympodial branching but always grow on for several seasons before the apex dies off (tab. 2: XI 1,2).
- Anthetic-sympodial shoot systems (I/3) only rarely bear uniflorous RUs (II/5). In contrast they are characterized by cephaloids, truncate cephaloids and compound inflorescences (II/2-4). They predominantly show a regular sympodial branching pattern, each SU terminating in a terminal RU (light grey; tab. 2: XI 3).
- Flexible shoot systems (I/2) facultatively show a terminal RU at the end of the RS. As ananthic sympodia (I/1) they always include monopodial units and as anthetic sympodia (I/3) their RUs correspond to cephaloids and truncate cephaloids.

The close correlation between both the organization of the woody shoot systems and the structure of the inflorescences is an unexpected surprise. Accepting that both levels of complexity actually evolve independently from each other, the correlation may point to different evolutionary levels within the family. Genera with supposed primitive inflorescences also show a supposed primitive position of the RUs, while genera bearing truncate inflorescences always show the supposed advanced terminal position of the RUs concerned.

Based on inflorescence morphological data a preliminary intergeneric arrangement of the Bruniaceae is given (fig. 242, 243). *Thamnea/Mniothamnea*, the '*Audouinia*-group', *Berzelia* and *Brunia* are all thought to be basal groups. *Raspalia* appears to have a central position in case all truncate RUs would have derived from this genus. There is no genus with clearly appears as the most advanced one though in *Nebelia* compound and in *Staavia* flower-like RUs have evolved.

Niedenzu & Harms (1930) subdivided the Bruniaceae into the Audouinieae (*Audouinia, Tittmannia, Thamnea*) and the Brunioideae (remaining genera) based on anther morphology. Later on, Takhtajan (1987) modified the classification by keeping the

- Audouinieae and subdividing the Brunioideae into the
- Lonchostomoideae with *Lonchostoma* being thought to have a sympetalous corolla, the
- Berzelioideae including the two unilocular genera *Mniothamnea* and *Berzelia* and the
- Brunioideae comprising the remaining genera.

The close relationship between *Audouinia* and *Tittmannia* could be confirmed by the present study, but *Thamnea*, also belonging to the Audouinieae sensu Niedenzu & Harms (1930) appears to be quite different relative to inflorescence morphological data. *Linconia*, in contrary, shares inflorescence morphological characters with *Audouinia* and *Tittmannia*.

As regards *Pseudobaeckea teres* there are many characters which point to an incorrect position. Dümmer (1912) excluded the species from *Brunia* and placed it into *Pseudobaeckea* though he already noticed the differences between *P. teres* and the remaining species. Pillans (1947) mentioned that the species would be better placed in *Raspalia*, but palynological (Hall 1988, fig. 244) and leaf anatomical data (Carlquist 1991, fig. 244)) pointed to a close relationship to *Audouinia* and *Tittmannia*. This is confirmed by the present study. As a result, *Pseudobaeckea teres* is preliminarily included into *Tittmannia* (fig. 242).

The separation of *Lonchostoma* appears to be groundless following Leinfellner (1964a) who found the corolla in *Lonchostoma* to be 'pseudosympetalous'. The corolla tube in fact results from an alternate fusion of petals and filaments. In view of the manifold differences between *Mniothamnea* and *Berzelia* it is likewise doubted that both form a natural group. It has rather to be considered that the numerical reduction in the ovary might have happened repeatedly in the family.

Since the time of Niedenzu & Harms (1930) the increasing knowledge of the family has repeatedly resulted in intergeneric rearrangements (Pillans 1947, Goldblatt 1981, Takhtajan 1987, Hall 1988, Carlquist 1994):

- Pillans (1947; fig. 4) arranged the genera relative to the morphology of inflorescence and ovary structures. He held the monotypic *Audouinia*, which is the only one bearing a trilocular ovary, to be the basal group, *Raspalia* the central and *Berzelia* (unilocular, uniovulate) the most derived genus of the family. Compared with the present study it is interesting that Pillans interpreted the terminal inflorescences of *Pseudobaeckea* and *Lonchostoma* to be composed of axillary flowers, while *Raspalia*, *Nebelia* and *Staavia* are characterized as having capitate flower-arrangements. His interpretation would support the discussed relationship between *Pseudobaeckea*, *Lonchostoma* and the '*Audouinia*-group' (fig. 242). However, following the present study the advanced position of *Berzelia* could not be confirmed.

- Leinfellner (1964b) studied petal morphology in Bruniaceae. He distinguished six groups relative to peltate-ascidial (1,2), peltate-diplophyllous (3,4) and rudimentary diplophyllous (5,6) petals:
  (1) *Audouinia capitata*
  (2) *Linconia* (three spec.), *Lonchostoma pentandrum*, *Pseudobaeckea africana*, *Tittmannia laxa*, *Raspalia microphylla*, *R. phylicoides*, *Staavia* (four spec.), *Mniothamnea callunoides*
  (3) *Raspalia. Angulata*
  (4) *Brunia laevis*, *B. nodiflora*, *B. macrocephala*
  (5) *Raspalia virgata*., *Berzelia* (five spec.), *Nebelia* (three spec.)
  (6) *Thamnea* (four spec.).

  The results presented by Leinfellner are only cited with reservations. As Leinfellner analysed selected species it is not clear how far the petal characters would correspond with the generic circumscriptions. Besides, the diplophyllous nature of an organ is very difficult to identify and therefore it seems reasonable to reexamine petal morphology before using the data for systematic purposes. However, his studies appear to confirm the basal position of *Audouinia* and the heterogenity of *Raspalia*.

- Goldblatt (1981) found n = 11 to be the basal chromosome number in the family. *Audouinia capitata* is the only of 23 studied species being diploid (2n = 22), 19 species are characterized by n = 22-23 or 2n = 40-46, while *Staavia radiata* and two *Berzelia* species show 2n = 80-86. *Berzelia intermedia*, one of the few common and widely distributed species, has both tetraploidic populations (2n ≈ 42) and those with an even higher grade of ploidy (2n = 80-86; ≈ 120). It is interesting that *Audouinia capitata* again appears at a basal position. Beyond that, the caryological data include no clear information relative to the intergeneric arrangement of the Bruniaceae

- Hall (1988) studied pollen morphology in Bruniaceae and found five groups:
  (1) tricolporate:
  Audouinia capitata, *Tittmannia*, *Pseudobaeckea teres*, *Thamnea* (three spec.), *Linconia*, *Berzelia*, *Brunia albiflora*, *B. stokoei*, *B. alopecuroides*
  (2) tri- to fivecolporate, foveolate:
  Thamnea diosmoides, *Mniothamnea*, *Raspalia* (ten spec.), *Staavia* (four spec.), *Nebelia* (three spec.), *Pseudobaeckea africana*, *P. cordata*
  (3) five- to sixcolporate, foveolate:
  Thamnea hirtella, *Raspalia globosa*, *R. sacculata*, *Nebelia stokoei*, *N. fragarioides*, *Staavia zeyheri*, *S. globosa*., *Lonchostoma esterhuyseniae*
  (4) five- to eightcolporate, psilate to reticulate, apiculate in equatorial view:
  Brunia (four spec.)
  (5) six- to tencolporate, verrucate to foveolate, oval in equatorial view:
  Lonchostoma (four spec.)

  The high palynological diversity points to repeated changes of pollen grain structures within the Bruniaceae (fig. 244). It confirms the basal position of the '*Audouinia*-group', *Thamnea* and

Berzelia. Beyond, it is interesting that both *Lonchostoma esterhuyseniae* and *Pseudobaeckea teres* differ from the remaining species of their genera and that *Brunia* shows two different pollen morphologies. These findings exactly correspond to the results of the present morphological study.

As regards *Brunia*, the genus appears to be heterogenous. *Brunia laevis, B. nodiflora, B. neglecta* and *B. macrocephala* are characterized by a zygomorphic androecium, a pair of biovulate carpels, 5-8 colporate pollen grains and a continuous leaf metamorphosis (tab. 2), while *Brunia albiflora, B. stokoei* and *B. alopecuroides* have equal stamens, a unilocular uniovulate ovary, tricolporate pollen grains and an abrupt metamorphosis. The latter species completely correpond to *Berzelia* where they are preliminarily incorporated in the present study. Except *B. albiflora* which very rarely bears terminal inflorescences and thus has to be grouped with the anthetic species all *Berzelia* plus the added *Brunia* species are ananthic while the remaining *Brunia* species show the supposed change from ananthic via flexible to anthetic conditions.

The similarity between *Brunia* and *Berzelia* might have been caused by a common ancestor being characterized by cephaloids arranged in unspecialized ananthic sympodia. In *Berzelia* specialization between vegetative and inflorescence shoots was increased promoting the ananthic condition. Besides both the number of locules and the number of ovules were reduced to one. In *Brunia* s.str. specialization increased relative to flower symmetry and pollen grain structures. The gradual extension of the reproductive impulse resulted in terminal inflorescences characterizing anthetic shoot systems. In *Brunia macrocephala* usually only the terminal RU is present while the branching zone of the RS remains unbranched or only bears vegetative shoots (tab. 2 VIII, IX).

- Carlquist (1991) distinguished two groups relative to leaf anatomical characters
  (1) *Audouinia, Tittmannia, Pseudobaeckea teres, Thamnea, Berzelia, Brunia, Nebelia* (large strand of fibres on the midvein; rhomboidal crystals in bundle sheath cells)
  (2) *Linconia, Mniothamnea, Raspalia, Staavia, Pseudobaeckea, Lonchostoma* (few or no fibres on veins; druses in mesophyll cells).

Because of the unusual combination of the characters, Carlquist held the opinion that the grouping might reflect a natural subdivision of the family (fig. 244A,B). It confirms the Audouinieae sensu Niedenzu & Harms (1930), but does not confirm the Berzelioideae sensu Takhtajan (1987). Compared with the present study it is interesting that *Pseudobaeckea teres* differs from the remaining species of the genus. Following Carlquist (1991) this species corresponds to *Audouinia, Tittmannia* and *Linconia* in bearing a rim around the cuticular domes overlying the guard cells. Despite this conformity which appears to confirm the '*Audouinia*-group' *Linconia* does not share the anatomical characters listed above with this group. The findings of Carlquist (1991) largely correspond to the inflorescence morphological data in combining the supposed primitive genera *Audouinia, Tittmannia* (including *Pseudobaeckea teres*), *Berzelia*, and *Thamnea*. But, accepting that the leaf anatomical data would reflect two natural subfamilial groups, they also separate *Linconia* from the '*Audouinia*'-group and the two uniflorous genera *Thamnea* and *Mniothamnea* from each other. The change from rhomboidal cristals in bundle sheat cells to druses in mesophyll cells might have originated from *Brunia* s.str. If this is true, uniflory and truncate RUs (arrows) have evolved repeatedly within the family.

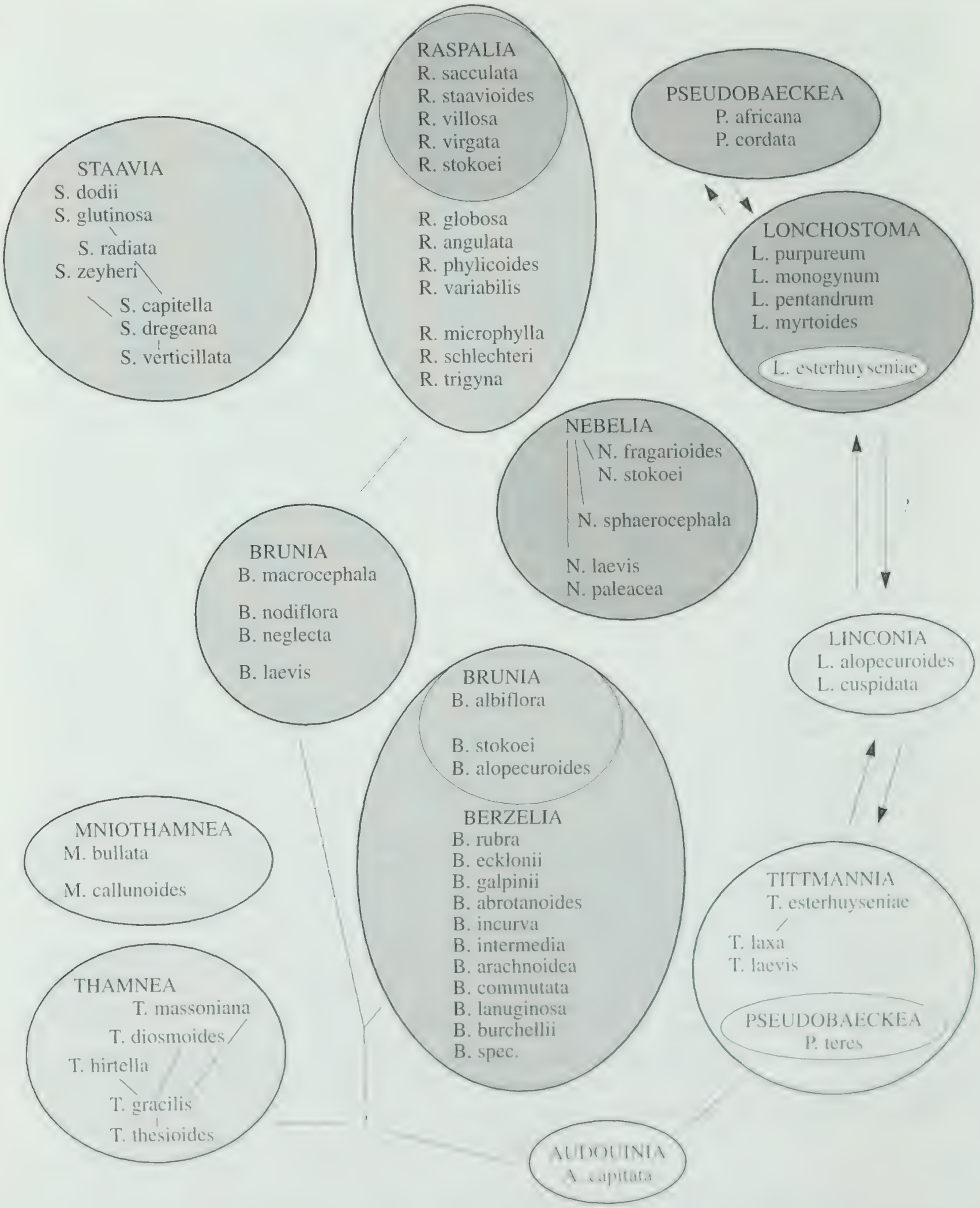


Figure 242 ***Preliminary intergeneric arrangement of the Bruniaceae*** *based on inflorescence morphological characters. The '* Audouinia*-group', Berzelia,* Brunia *and* Thamnea *are all thought to be basal groups. Three* Brunia *species have been incorporated into* Berzelia *and* Pseudobaeckea teres *into Tittmannia. The position of* Lonchostoma esterhuyseniae *is not clear and likewise the relation of both* Lonchostoma *and* Pseudobaeckea *to* Linconia. *Within the genera the species are arranged following further morphological characters, e.g position, complexity and flower-like appearance of the RU (see tab. 2).*

*Grey gradations (from light to dark: '*Audouinia *group' (II 1),* Thamnea/Mniothamnea *(II 5), 'cephaloid-group' (II 2), 'truncate cephaloid-group'(II 3,4); question-mark: supposed position of ancestral form; question-mark and black arrows: unknown relation between* Linconia *and* Lonchostoma*. grey arrows: unclear relations*

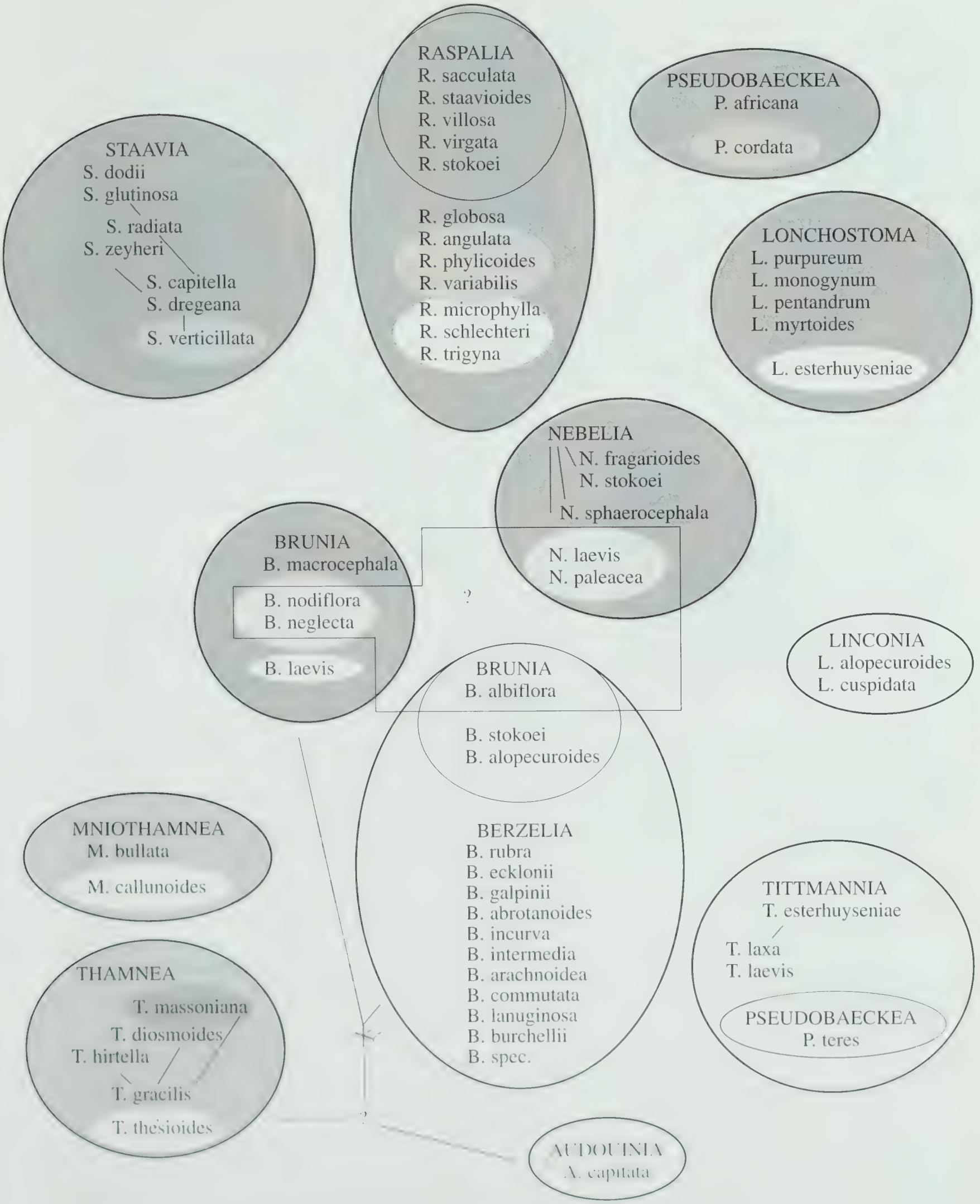


Figure 243 ***The position of the RUs in Bruniaceae*** *projected onto the preliminary arrangement (compare with fig. 242)*

Grey gradations (from light to dark):groups of different RU-position (see tab. 3): always lateral (I/1), flexible (II/2), terminal (II/3) referred to the SU (3a) and the SGU (3b).

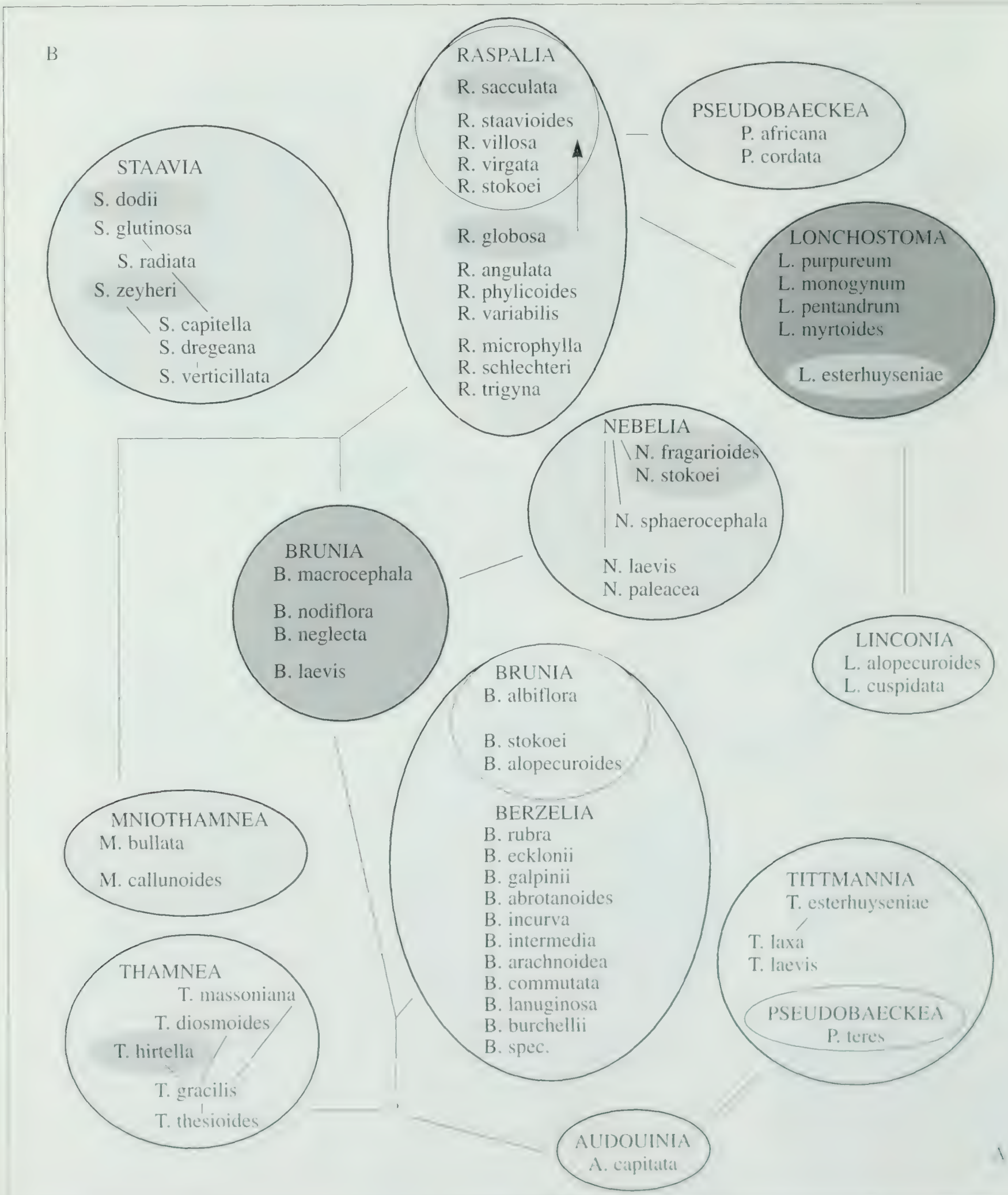


Figure 244 ***Palynological and leaf anatomical data*** *of the Bruniaceae projected onto the preliminary arrangement (compare with fig. 242). Note that pollen grain structures appear to have repeatedly changed within the family and that uniflory and truncate RL's have evolved several times in case the leaf anatomical data really reflect a natural subdivision.*

Grey gradations (from light to dark): groups of different pollen grains following Hall 1988 (see text, p. 298); A, B, groups of different leaf anatomy following Carlquist 1991 (see text, p. 299); lines: possible relations between individual taxa considering that the two leaf anatomical groups (A,B) really reflect natural groups, arrows: truncation

5.3 Outlook

The high diversity among the recent members of the Bruniaceae illustrate that the present species are all derived in one or more characters. This appears to be even true for *Audouinia capitata* whose basal position is largely undisputed. It thus might be justified to propose a common already extinct ancestor. However there is no clear knowledge about the origin of the Bruniaceae neither about their nearest relatives nor about their original geographic range. Except the rbcL-sequences of only two species no molecular data have been published until now.

Growth form and inflorescence structure of the Bruniaceae were described in detail in the present study. The high diversity in the family caused the general discussion on inflorescences in woody plants and the `brunioid´ reference framework. The reason for not interpreting the data in an ecological manner is the lack of any specific knowledge about the biology of Bruniaceae. With the exception of the profound autecological study in *Audouinia capitata* no field investigations were made until now.

Besides the many new morphological data presented here the study has raised several questions, in particular whether *Audouinia* really is the basal genus, whether the uniflorous RUs of the *Audouinia*-group and of *Thamnea/Mniothamnea* represent primitive or derived stages, whether the latter two genera form a natural group or not, whether *Lonchostoma* and *Pseudobaeckea* do have true truncate inflorescences or in fact masked aggregates of individual RUs, and whether the indeterminate inflorescences evolved only once, namely in *Raspalia,* or repeatedly in the family.

In view of the many preliminary statements it is intended to extend the research in Bruniaceae. In particular molecular studies have been initiated to elucidate the phylogeny of the family. The data should also help to reconstruct the evolution of morphological characters and to test the newly introduced reference framework. Studies on flower, seed and fruit morphology are in progress. To explain the diversity within the family it is furthermore intended to add field investigations covering the biology of pollination and fruit dispersal, the vegetative and sexual reproduction and the influence of abiotic factors on the growth form and life cycle of the Bruniaceae.

The final aim of the research will be to reconstruct the evolution of the Bruniaceae and to explain the present diversity. Both is particularly interesting because the family appears to have passed a long evolutionary history and to have radiated in a manifold manner. Considering the species and niches richness of the Cape floral kingdom some general conclusions on the evolution and distribution pattern of endemic South African plants are also expected.

6

References

Anonymus (1987) - Wild flowers of South Africa. Cape Town: Struik.

Backlund, A., Gustafsson, M.H.G. & Bremer, B. (1996) - Phylogeny of the Asteridae s. str. based on *rbc*L sequences, with particular reference to the Dipsacales. In Backlund, A.: Phylogeny of the Dipsacales. Uppsala University 1996.

Barthélémy, D. (1988) - Architecture et sexualité chez quelques plantes tropicales: le concept de floraison automatique. *Thèse de Doctorat, Université de Montpellier II, France.*

Bayer, C. (1994) - Zur Infloreszenzmorphologie der Malvales. *Diss. Bot.* **212**. Berlin, Stuttgart: Cramer.

Bell, A.D. (1991) - Plant Form: An illustrated guide to flowering plant morphology. Oxford University Press.

Bond, P. & Goldblatt, P. (1984) - Plants of the Cape Flora - a descriptive catalogue. *J. S. Afr. Bot. Suppl. Vol.* **13**.

Briggs, B. & Johnson, L. (1979) - Evolution in the Myrtaceae - evidence from inflorescence structure. *Proc. Linn. Soc. New South Wales* **192**: 157-272.

Briggs, B. & Johnson, L. (1982) - Inflorescences . a further comment. *Austr. Syst. Bot. Soc. Newsletter* **30:** 57-58.

Burman, L. & Bean, A. (1985) - Hottentots Holland to Hermanus. *South African Wild Flower Guide* **5**. Kirstenbosch: Botanical Society of South Africa.

Carlquist, S. (1978) - Wood anatomy of Bruniaceae: correlations with ecology, phenology and organography. *Aliso* **9**: 323-364.

Carlquist, S. (1991) - Leaf anatomy of Bruniaceae: ecological, systematic and phylogenetic aspects. *Bot. J. Linn. Soc.* **107**: 1-34.

Celakovsky, L.J. (1893) - Gedanken über eine zeitgemäße Reform der Theorie der Blütenstände. *Bot. Jahrb. Syst.* **16:** 32-51.

Claßen, R. (1984) - Untersuchungen zur Struktur und Phylogenie von Pseudanthien unter besonderer Berücksichtigung ihrer Analogie zu zoophilen Einzelblüten. *Dissertation Rheinisch-Westfälische Technische Hochschule Aachen, Germany.*

Claßen, R. (1988) - Beiträge zur Kenntnis der Gattung Lasiopetalum (Sterculiaceae). *Bot. Jahrb. Syst.* **109**: 501-527.

Claßen-Bockhoff, R. (1992) - (Prä-)Disposition, Variation und Bewährung am Beispiel der Infloreszenzblumenbildung. *Mitt Hamb. Zool. Mus. Inst.* **89, Suppl. 1** (34. Phylogenetisches Symposium): 37-72.

Claßen-Bockhoff, R. (1994) - Verzweigungsverhalten und Infloreszenzstruktur der Bruniaceen: systematische, morphologische aund phylogenetische Schlußfolgerungen. *Habilitationsschrift Rheinisch-Westfälische Technische Hochschule Aachen, Germany.*

Claßen-Bockhoff, R. (1995a) - Ein neues Bezugssystem zur Homologisierung von Blütenständen bei Holzgewächsen am Beispiel der Bruniaceae. - Kurzfassungen 12. Symposium `Morphologie, Anatomie und Systematik Mainz: 11.

Claßen-Bockhoff, R. (1995b) - Wuchsverhalten und Infloreszenzstruktur in der Gattung Nebelia (Bruniaceae). *Feddes Repertorium* **106**: 415-437.

Claßen-Bockhoff, R. (1996) - Functional units beyond the level of the capitulum and cypsela in Compositae. In Cagliari, P.D.S. & Hind, D.J.N. (eds.), Compositae: Biology & Utilization. Proceedings of the International Compositae Conference, Kew, 1994, vol.2: 129-160, Royal Botanic Gardens, Kew.

Claßen-Bockhoff, R. (1999) - Pflanzenmorphologie - 200 Jahre nach Goethe. *Abstracts of the 14th symposium of the German Botanical Society section 'Biodiversität und Evolutionsbiologie' Jena*: 39.

Claßen-Bockhoff, R. (in press) - Bruniaceae. In: Kadereit. J.W. (ed.), The families and genera of vascular plants, Vol. Asteridae II.

Crane, P.R., Friis, E.M. & Pedersen, K.R. (1995) - The origin and early diversification of angiosperms. *Nature* **374**: 27-33.

Cremers, G. (1974) - Architecture de quelques lianes d'Afrique Tropicale. 2. *Candollea* **29**: 57-110.

Cronquist, A. (1981) - An integrated system of classification of flowering plants. *Columbia Univ. Press*, New York.

Cronquist, A. (1988) - The evolution and classification of flowering plants. 2nd edit. New York Botanical Garden.

Dahlgren, R. & Van Wyk, A.E. (1988) - Structures and relationships of families endemic to or centered in South Africa. 5. Bruniaceae A.P. de Candolle. In: Goldblatt, P. & Lowry, P.P. (Eds.), Modern systematic studies in African botany. *Monogr. Syst. Bot. Miss. Bot. Gard.* **25**: 1-94.

De Lange, J.H. & Boucher, C. (1990) - Autecological studies on Audouinia capitata (Bruniaceae). 1. Plant-derived smoke as a seed germination cue. *S. Afr. J. Bot.* **56:** 700-703.

De Lange, J.H. & Boucher, C. (1993a) - Autecological studies on Audouinia capitata (Bruniaceae). 4. Seed production, seed banks and seedling recruitment. *S. Afr. J. Bot.* **59**: 145-155.

De Lange, J.H. & Boucher, C. (1993b) - Autecological studies on Audouinia capitata (Bruniaceae). 8. Role of fire in regeneration. *S. Afr. J. Bot.* **59**: 188-202.

De Lange, J.H. & Boucher, C. (1993c) - Stimulation of in vitro pollen germination in Audouinia capitata by the simultaneous use of several carbohydrates. *S. Afr. J. Bot.* **59**: 270-272.

De Lange, J.H., Boucher, C. & Van der Walt, J.J.A. (1993d) - Autecological studies on Audouinia capitata (Bruniaceae). 3. Pollination biology. *S. Afr. J. Bot.* **59**: 135-144.

De Lange, J.H., Van der Walt, J.J.A. & Boucher, C. (1993e) - Autecological studies on Audouinia capitata (Bruniaceae). 5. Seed development, abortion and pre-emergent reproductive success. *S. Afr J. Bot.* **59:** 156-167.

De Lange, J.H., Van der Walt, J.J.A. & Boucher, C. (1993f) - Autecological studies on Audouinia capitata (Bruniaceae). 6. Nutritional aspects of the developing ovule. *S. Afr. J. Bot.* **59**: 168-177

De Lange, J.H., Thompson, G.R. & Swart, C.R. (1993g) - Autecological studies on Audouinia capitata (Bruniaceae). 7. Nutritional aspects in the mature seed. *S. Afr. J. Bot.* **59:** 178-187.

Drénou, C. (1994) - Approche architecturale de la sénescence des arbres. Les cas de quelques angiospermes tempérées et tropicale. Thèse Doct., Univ. Montpellier II.

Dümmer, R.A., 1912: An enumeration of the Bruniaceae. *Journ. Bot.* **50, Suppl.2**: 1-37.

Dyer, R.A. (1944) - Brunia albiflora. *Fl. Pl. S. Afr.* **24**: pl. 928.

Edelin, C. (1977) - Images de l'architecture des Conifères. *Th. Doct. 3° cycle, Univ. Montpellier II.*

Edelin, C. (1991) (ed.) - L'Arbre. Biologie et dévelopement. *Naturalia Monspellensia* **A7**: 127-154

Endress, P.K. (1970) - Die Infloreszenzen der apetalen Hamamelidaceen, ihre grundsatzliche morphologische und systematische Bedeutung. *Bot. Jahrb. Syst.* **90**: 1-54.

Froebe, H.A. & Gleißner, P. (1995) - Die Organisationseinheit als Bezugselement für die Strukturanalyse von verholzenden Sproßsystemen. *Feddes Repertorium* **106**: 391-406.

Gleißner, P. (1998) - Das Verzweigungsmuster ausgewählter Laubbaumarten und seine Veranderung durch nicht-pathogene Schädigungen. *Palmarium Hortus Francofurtensis* **6**: 3-132.

Goebel, K. (1928) - Organographie der Pflanzen. Vol. I., 3rd edit. Jena.

Goebel, K. (1931) - Blütenbildung und Sproßgestaltung (Anthokladien und Infloreszenzen) Organographie der Pflanzen, 2. Ergbd. Jena.

Hagemann, I. (1989) - Wuchsformen einiger Hypericum-Arten, ein Beitrag zum morphologischen und zum ökologischen Anliegen der Wuchsformen-Forschung. *Flora* **183**: 225-309.

Hall, A.V. (1987a) - Evidence of a Cretaceous alliance for the Bruniaceae. *S. Afr. J. Sci.* **83**: 58-59

Hall, A.V. (1987b) - Bruniaceae. In Gibbs-Russell, G.E., Welman, W.G., Retief, E., Immelmann, K.L., Germishuizen, G., Pienaar, B.J., Van Wyk, M. & Nicholas, A.: List of species of Southern African plants. 2nd edit. Part 2, *Mem. Bot. Surv. S. Afr.* **56**: 62-63.

Hall, A.V. (1988) - Systematic palynology of the Bruniaceae. *Bot. J. Linn. Soc.* **96**: 285-296.

Hallé, F. (1986) - Modular growth in seed plants. *Phil. Trans. R. Soc. Lond.* **B 313**: 77-87.

Hallé, F. & Martin, R. (1968) - Etude de la croissance rythmique chez l'Hévéa (Hevea brasiliensis Müll. Arg. Euphorbiacées-Crotonoidées). *Adansonia (N.S.)* **8**: 475-503.

Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) - Tropical trees and forests. An architectural analysis. Berlin, Heidelberg, New York: Springer.

Hallier, H. (1912) - L'origine et le système phylétique des angiosperms exposés à l'aide de leur arbre généalogique. *Arch. Néerl. Sci. Exact. Nat. , sér.* **3,1**: 146-234.

Hamann, U. (1958) - Morphologische und histogenetische Studien an Veronica-Arten. I. Zur Morphologie der Blütenstände im Hinblick auf einen allgemeinen Infloreszenzbegriff. *Bot. Jb.* **78:** 69-118.

Hamann, U. (1960) - Morphologische Beobachtungen an Hebe disomifolia (Scrophulariaceae), besonders ihren Infloreszenzen. *Bot. Jb.* **79**: 405-427.

Hauser, M. (1932) - Polarität und Blütenverteilung. *Bot. Abh.* **21**: 3-68.

Hilton-Taylor, C. (1996) - Red data list of South African plants. *Strelitzia* **4**.

Holländer, K. & Jäger, E.J. (1994) - Morphologie, Biologie und ökogeographische Differenzierung von Globularia. I. Progressionen in der Wuchsform, Infloreszenz, Blattnervatur und Verbreitung. *Flora* **189**: 223-254.

Humboldt, A.v. (1806) - Ideen zu einer Physiognomik der Gewächse. Berlin, Stuttgart.

Hutchinson, J. (1969) - Evolution and phylogeny of flowering plants. Dicotyledons: Facts and theory. Academic Press, London.

Jäger, E.J. (1980) - Progressionen im Synfloreszenzbau und in der Verbreitung bei den Betulaceen. *Flora* **170**: 91-113.

Jahnke, C. (1986) - Der Infloreszenzbau der Cornaceen sensu lato und seine systematischen Konsequenzen. *Abh. Akad. Wiss. Lit. Mainz, math.-naturw. Kl., Reihe trop. u. subtrop. Pflanzenwelt* **57**.

Judd, W.S., Campbell, C.S., Kellogg, E., A. & Stevens, P.F. (1999) - Plant systematics. A phylogenetic approach. Sunderland: Sinauer.

Kaussmann, B. (1954) - Die Entwicklung des echten Ehrenpreis (Veronica officinalis). *Archiv d. Freunde d. Naturgeschichte in Mecklenburg* **1**: 81-95.

Kubitzki, K., Rohwer, J.G. & Bittrich, V. (1993) - The families and genera of vascular plants. II. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families. Berlin, Heidelberg, New York: Springer.

Kuhn, T. S. (1976) - Die Struktur wissenschaftlicher Revolutionen. 2nd edit. Frankfurt: Suhrkamp.

Kunze, H. (1985) - Die Infloreszenzen der Marantaceen und ihr Zusammenhang mit dem Typus der Zingiberales-Synfloreszenz. *Beitr. Biol. Pfl.* **60**: 93-154.

Kunze, H. (1989) - Probleme der Infloreszenztypologie von W. Troll. *Plant Syst. Evol.* **163:** 187-199.

Kusnetzova, T.V. (1988) - Angiosperm inflorescences and different types of their structural organization. *Flora* **181**: 1-17.

Leinfellner, W. (1964a) - Über die falsche Sympetalie bei Lonchostoma und anderen Gattungen der Bruniaceen . *Österr. Bot. Z.* **111**: 345-353.

Leinfellner, W. (1964b) - Sind die Kronblätter der Bruniaceae peltat gebaut? *Österr. Bot. Z* **111**:500-526.

Le Roux, A , Kyriacou, X.L & Orshan, G. (1984) - The pheno-morphology of selected plants in mediterranean-type ecosystems of South Africa. *Bull. Soc. Bot. Fr.* **131**, *Actual. Bot.*: 441-450.

Maresquelle, H J (1970) - Le thème évolutif des complexes d'inflorescences. Son aptitude à susciter des problèmes nouveaux. *Bull. Soc. Bot. France* **117**: 1-4.

Maresquelle, H J (1977) - Architektonische Morphologie der Höheren Pflanzen als Ausdruck eines Korrelationsnetzes. *Ber. Deutsch. Bot. Ges.* **90**: 309-323.

Maresquelle, H.J. & Sell, Y. (1965) - Les problèmes physiologiques de la floraison descendante. *Bull. Soc. Physiol. végét.* **11**: 94-98.

Meusel, H. (1951) - Die Bedeutung der Wuchsform für die Entwicklung des natürlichen Systems der Pflanzen. Feddes Repert. **54**: 137-172.

Moll, E.J. & Gubb, A.A. (1981) - Aspects of the ecology of Staavia dodii in the South Western Cape of South Africa. In: Synge, H. (ed): The biological aspects of rare plant conservation: 331-342. - Wiley & Sons Ltd.

Müller-Doblies, D. & Weberling, F. (1984) - Über Prolepsis und verwandte Begriffe. *Beitr. Biol. Pflanzen* **59**: 121-144.

Nel, J.P. (1986) - Ontekologiese studie van Berzelia lanuginosa, Brunia nodiflora en Nebelia paleacea (Bruniaceae). B.Sc. (Hons.), unpublished, University of Stellenbosch.

Niedenzu, F. & Harms, H. (1930) - Bruniaceae. In: Engler, A. & Prantl, K. (eds.): Die natürlichen Pflanzenfamilien. Ed. 2, 18a. Leipzig: Engelmann, pp: 288-303.

Olmstead, R.G., Bremer, B., Scott, K.M. & Palmer, J.D. (1993) - A parsimony analysis of the Asteridae sensu lato based on rbcL sequences. *Ann. Missouri Bot. Gard.* **80**: 700-722.

Pankhurst, R.J. (1984) - On the description of inflorescences. In Allkin, R. & Bisby, F. (eds.), Databases in systematics: 309-320. London and Orlando: Academic Press.

Parkin, J. (1914) - The evolution of the inflorescence. *Linn. Soc. Bot. London* **42**: 511-563.

Pilger, R. (1921) - Bemerkungen zur phylogenetische Entwicklung der Blütenstände. *Bericht der Freien Vereinigung für Pflanzengeographie und systematische Botanik für das Jahr 1919*: 69-77. Berlin.

Pilger, R. (1922) - Über Verzweigung und Blütenstandsbildung bei den Holzgewächsen. *Bibl. Bot.* **90**: 1-38.

Pillans, N.S. (1947) - A revision of Bruniaceae. *J. S. Afr. Bot.* **13**: 121-206.

Powrie, E. (1969) - A new species of Tittmannia (Bruniaceae). *Jl. S. Afr. Bot.* **35**: 363-366.

Prévost, M.F. (1967) - Architecture de quelques Apocynacées ligneuses. *Mém. Soc. Bot. Fr.* **114**: 23-36.

Rauh, W. (1939) - Über die Gesetzmäßigkeit der Verzweigung und deren Bedeutung für die Wuchsformen der Pflanzen. *Mitt. Dt. Dendrol. Ges.* **52**: 86-111, plates 21-26.

Rauh, W. (1975) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 90-101.

Rickett, H.W. (1944) - The classification of the inflorescences. *Bot. Rev.* **10**: 187-231.

Rickett, H.W. (1955) - Materials for a dictionary of botanical terms. III. Inflorescences. *Bull. Torr. Bot. Club* **82**: 419-445.

Schröder, F.-G. (1987) - Infloreszenzen, Synfloreszenzen und Moduln. Ein terminologischer Beitrag zur Infloreszenzmorphologie. *Bot. Jahrb. Syst.* **108**: 449-471.

Schützsack, U. (1965) - Die morphologischen Grundlagen der Blührhythmik der Hamamelidaceae *Willdenowia*, **Beiheft 3.**

Scott, G. (1989) - Bravo for the Bruniaceae. *Veld & Flora* **75**: 104-106.

Sell, Y. (1969) - Les complexes inflorescentiels de quelques Acanthacées Etude particulière des phénomènes de condensation, de racémisation, d'homogénéisation et de troncure *Ann. Sci. nat., Bot. et Biol. végét.*, **12e ser., 10**: 225-350.

Sell, Y. (1976) - Tendances évolutives parmi les complexes inflorescentiels *Rev. Gen. Bot.* **83**: 247-267.

Sell, Y. (1980) - Physiological and phylogenetic significance of the direction of flowering in inflorescence complexes. *Flora* **169**: 282-294.

Sell, Y. (1982) - Die komplexen racemösen Infloreszenzstrukturen bei einigen Myrtalen. *Beitr. Biol. Pfl.* **56**: 381-414.

Sell, Y. (1995) - Recherches de critères pour déterminer la limite entre les domaines végétatif et floral. *Feddes repert.* **106**: 371-390.

Sell, Y. & Cremers, G. (1992) - The reiteration of the miniaturised model in some complex inflorescences. *Flora* **187**: 51-59.

Sell, Y. & Cremers, G. (1994) - Identification de l'unité de floraison des Marantacées. *Beitr. Biol. Pfl.* **68**: 27-49

Stauffer, H.U. (1963) - Gestaltwandel bei Blütenständen von Dicotyledonen . *Bot. Jahrb. Syst.* **82**: 216-251.

Stebbins, G.L. (1973) - Evolutionary trends in the inflorescences of Angiosperms. *Flora* **162**: 501-528.

Strid, A. (1968) - A new species of Lonchostoma (Bruniaceae). *Bot. Not.* **121**: 312-316.

Takhtajan, A. (1973) - Evolution und Ausbreitung der Blütenpflanzen. Stuttgart: Fischer.

Takhtajan, A. (1976) - Neoteny and the origin of flowering plants. In Beck, C.B. (ed.): Origin and Early Evolution of Angiosperms: 207-219. New York, London: Columbia Univ. Press.

Takhtajan, A. (1980) - Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev. (Lancaster)* **46**: 225-359.

Takhtajan, A. (1987) - Systema Magnoliophytorum. Leningrad, Officina Editoria Nauka.

Takhtajan, A. (1991) - Evolutionary trends in flowering plants. New York: Columbia University Press.

Thaler, I. (1951) - Morphologisches über Veronica filiformis Smith und ihre Verwandten. *Phyton (Horn)* **3**: 216-226.

Thorne, R.F. (1976) - A phylogenetic classification of the Angiospermae. *Evol. Biol.* **9**: 36-106.

Thorne, R.F. (1983) - Proposed new realignements in the Angiosperma. *Nordic J. Bot.* **3**: 85-117.

Tissot, M. & Weberling, F. (1993) - Infloreszenzuntersuchungen an Leguminoseae-Caesalpinioideae. *Abh. Akad. Wiss. Lit. Mainz, math.-naturw. Kl., Reihe trop. und subtrop. Pflanzenwelt* **84**.

Troll, W. (1925) - Gestalt und Gesetz. Versuch einer geisteswissenschaftlichen Grundlegung der morphologischen und physiologischen Forschung. *Flora* **118/119**: 536-565.

Troll, W. (1928) - Organisation und Gestalt im Bereich der Blüte. *Monographien aus dem Gesamtgebiet der wissenschaftlichen Botanik,* **Bd. 1**.Berlin: Springer.

Troll, W. (1937) - Vergleichende Morphologie der höheren Pflanzen. Bd. I,1: Vegetationsorgane. Berlin: Bomtraeger.

Troll, W. (1941) - Gestalt und Urbild. Gesammelte Aufsätze zu Grundfragen der organischen Morphologie. In Pinder, W., Troll, W & Wolf, K.L. (eds.): Die Gestalt, Abhandlungen zu einer allgemeinen Morphologie, Heft 2. Halle: Niemeyer.

Troll, W. (1951) - Botanische Notizen II. *Abh. Akad. Wiss. Lit. Mainz, math.- nat. Kl.* Nr. **2**.

Troll, W. (1954) - Praktische Einführung in die Pflanzenmorphologie. Ein Hilfsbuch für den botanischen Unterricht und für das Selbststudium. 1. Teil: Der vegetative Aufbau. Jena: Fischer.

Troll, W. (1962) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz:* 86-104.

Troll, W. (1964a) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 93-111.

Troll, W. (1964b) - Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers. Bd. I. Jena: Fischer.

Troll, W. (1965) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 109-133.

Troll, W. (1967) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 89-103.

Troll, W. (1968) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 88-109.

Troll, W. (1969a) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 82-101.

Troll, W. (1969b) - Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers. Bd. II./1. Jena: Fischer.

Troll, W (1970) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 109-123.

Troll, W. (1971) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 107-127.

Troll, W. (1972) - Kommission für Biologische Forschung. *Jb. Akad. Wiss. Lit. Mainz*: 98-109.

Van Steenis, C G.G.J. (1963) - Definition of the concept 'inflorescence' with special reference to ligneous plants. *Flora Malesiana Bull.* **18:** 1005-1007.

Van Tieghem, T (1897) - Sur les caractères et les affinités des Grubbiacées. *J. Bot. (Morot)* **11**: 127-138.

Walter, H (1968) - Die Vegetation der Erde Bd 2: Die gemäßigten und arktischen Zonen in ökophysiologischer Betrachtung. Stuttgart: Fischer.

Weberling, F (1963) - Homologien im Infloreszenzbereich und ihr systematischer Wert. *Ber. Dt. Bot. Ges.* **76**: 1. Gen.vers. H.: 102-112.

Weberling, F. (1965) - Typology of inflorescences. *J. Linn. Soc. Bot. London*: **59**: 215-221, 1 plate.

Weberling, F. (1971) - Die Bedeutung der Infloreszenzmorphologie für die Systematik. *Ber. Dt. Bot Ges.* **84**:179-181.

Weberling, F. (1977) - Beiträge zur Morphologie der Rubiaceen-Infloreszenzen. *Ber. Dt. Bot. Ges.* **90**: 191-209.

Weberling, F. (1981) - Morphologie der Blüten und der Blütenstände. Stuttgart: Ulmer.

Weberling, F. (1982) - Current problems of modern inflorescence morphology. *Austral. Syst. Bot. Soc. Newsletter* **30**: 5-21.

Weberling. F. (1983a) - Evolutionstendenzen bei Blütenständen. *Abh. Akad. Wiss. Lit. Mainz. math.-naturw. Kl.* **Jg. 1983,1**: 5-32.

Weberling, F. (1983b) - Fundamental features of modern inflorescence morphology. *Bothalia* **14**: 917-922.

Weberling, F. (1985) - Zur Infloreszenzmorphologie der Lauraceae. *Bot. Jahrb. Syst.* **107**: 395-414.

Weberling, F. (1988a) - The architecture of inflorescences in the Myrtales. *Ann. Miss. Bot. Gard.* **75**: 226-310.

Weberling, F. (1988b) - Inflorescence structure in primitive Angiosperms. *Taxon* **37:** 657-690.

Weberling, F. (1989) - Morphology of flowers and inflorescences. Cambridge Univ. Press.

Weberling, F. (1992) - Primitive Blütenstände bei primitiven Angiospermen? *Stapfia* **28**. 29-51.

Weberling, F. & Herkommer, U. (1989) - Untersuchungen zur Infloreszenzmorpholgie der Thymelaeaceae. *Abh. Akad. Wiss. Lit. Mainz, math.-naturw. Kl., Reihe trop. und subtrop. Pflanzenwelt* **68**.

Weberling, F. & Troll, W. (1998) - Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers. Bd. II/2. Monotele und polytele Synfloreszenzen. Jena: Fischer.

Wolff, M.G. (1990) - Success with Staavia dodii. *Veld & Flora* **76**: 48-49.

Wright, M.G., Visser, D. & De Lange, J.H. (1991) - Autecological studies on Audouinia capitata (Bruniaceae). 2. Insects as pollen vectors *S. Afr. J. Bot.*. **57**: 260-263.

Zimmermann, W. (1965) - Die Blütenstände, ihr System und ihre Phylogenie. *Ber. Dt. Bot Ges.* **78**: 3-12.

After completion the following paper came to my knowledge:

Bradford, J.C. (1998) - A cladistic analysis of species groups in Weinmannia (Cunoniaceae) based on morphology and inflorescence architecture. *Ann.Missouri Bot. Gard.* **85**: 565-593.

Selected abbreviations

az	**a**pical **z**one
bz	**b**ranching **z**one
cfL	**c**ataleptic **f**lowering **L**ateral shoot
cfR	**c**ataleptic **f**lowering **R**enewal shoot
cR	**c**ataleptic **R**enewal shoot
dL	**d**eterminate **L**ateral shoot
En	***En**richment*
fz	**f**lowering **z**one
H	***H**omogenization*
ipi	**i**nflorescence **p**rimordium **i**nhibited
iL	**i**ndeterminate **L**ateral shoot
L	**L**ateral shoot
li	**l**ateral **i**nflorescence
lia	**l**ateral **a**ggregate of **i**nflorescences
mc	**m**onopodial **c**onnection
me	**me**sotony/mesotonic
n	growth period, season
R	**R**enewal shoot
RS	**R**eference **S**ystem
RU	**R**eproductive **U**nit
rz	**r**enewal **z**one
rz-1	**r**enewal **z**one of the parent axis
sc	**s**ympodial **c**onnection
sfL	**s**ylleptic **f**lowering **L**ateral shoot
sfR	**s**ylleptic **f**lowering **R**enewal shoot
SGU	**S**easonal **G**rowth **U**nit
SU	**S**ympodial **U**nit
svL	**s**ylleptic **v**egetative **L**ateral shoot
svR	**s**ylleptic **v**egetative **R**enewal shoot
T	***T**runcation*
tf	**t**erminal **f**lower
ti	**t**erminal **i**nflorescence
tia	**t**erminal **a**ggregate of **i**nflorescences
vz	**v**egetative **z**one
I, II, ..	orders of branches
', '', ..	orders of lateral structures/processes

Symbols

flower

inflorescence

aggregate of inflorescences

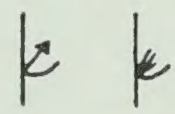
flower/inflorescence in bud

flower/inflorescence deflorated

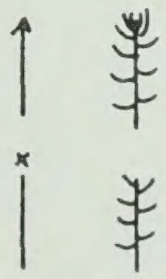
flowers/fruits fallen off

organs fallen off, missing

node with leaf



node with leaf and axillary bud



shoot with active apical meristem

shoot with inhibited apex

shoot broken off, damaged

shoot in graph interrupted

shoot in graph extended in length

Selected abbreviations and symbols,
see inside cover.

R. Claßen-Bockhoff

Opera Botanica Belgica | *Volume* 12

INFLORESCENCES IN BRUNIACEAE

WITH GENERAL COMMENTS ON INFLORESCENCES IN WOODY PLANTS

The present book not only increases our knowledge of the smal South African family Bruniaceae (12 genera / 75 species) but also deals with the simple but delicate question of how to delimitate inflorescences in woody plants. More than 80 % of the species of Bruniaceae are illustrated in detail by schematic side-views and photos (chapter 3). Referred to them the 'brunioid' reference framework is introduced (chapter 4). It differs from all concurrent concepts in strictly distinguishing caducous 'inflorescences' from persistent 'flowering shoot systems.' The study concludes with a summary of new insights into the intergeneric relationships of the Bruniaceae (chapter 5).

The present book includes a critical debate of the most important morphological concepts applied to inflorescences in woody plants (section 4.2). For that reason it is not only addressed to morphologists and Bruniaceae specialists, but might be of general interest to all dealing with inflorescences as to systematic, morphological, ecological, genetic and evolutionary aspects.

Regine Claßen-Bockhoff is a plant morphologist from the Johannes Gutenberg-University in Mainz (Germany). Since more than twenty years she is interested in form, function and evolution of inflorescences. Proceeding from the structural diversity of flower-like inflorescences she was engaged in individual families (e.g. Rubiaceae, Asteraceae) and theoretical questions being about ontogenetic and phylogenetic pathways of pattern repetition. Current projects deal with the diversity and evolution in the genus Salvia (Lamiaceae) and with interactions between architecture and sexual reproduction in Apiaceae.

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